ELEMENTARY BOTANY

W. WATSON

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An Introduction to the Study of Plant Life

BY

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PREFACE

This book is intended to be used as a companion to the student's work in the class-room, laboratory and field. The earlier chapters deal in an elementary way with some of the simpler phenomena of the flowering plant, whilst the later chapters are concerned with the less familiar groups of non-flowering plants. In order to give a wide and balanced outlook on the whole range of plant-life and, at the same time to keep the book to a convenient size for class-work, the later chapters have their subject-matter much more concentrated, though an attempt has been made to make the increase in difficulty a gradual one. An attempt is made to stimulate the reader to form his (or her) own conclusions from the data obtained by observations and experiments, and to test such conclusions by further work; the way to the pool of knowledge is shown, but the method of transit and acquisition must depend on personal initiative. A knowledge of plant-life may be more slowly acquired, but will rest upon sounder foundations than if a spoon-feeding method is adopted.

The general physiology of the plant is not dealt with in a separate chapter or chapters, but is associated with morphological features; the study of the methods of life are correlated with the structures which enable the plant to benefit by such methods.

A book for class-work must not be unwieldy, and the author is aware of the omission of many things which would have given a greater completeness to the story of plant-life. It is impossible in a work of this size to include all the links in the chain of the story, and the reader is sometimes referred

to works dealing with special portions of the story. Ecology is dealt with partly in two chapters and partly in scattered references, and the reader should be able to obtain some idea of the methods adopted in the systematic study of the subject. But no real knowledge of ecology can be obtained from a book ; a half-hour's talk by the side of a wall or other plant-habitat is of far more use than a number of set lectures.

Practical work is often suggested to the student, and the material for such work is taken from as common plants as possible. Examples of various structures, modifications, plant-groups, etc., are taken from British or commonly cultivated plants where possible, and among these from those most widely distributed.

Specific names are indicated by italics and, in accordance with the custom adopted by many ecologists, are never given with initial capitals. As advocated in some scientific journals, *andrecium* and *gynecium* are brought into agreement with each other in regard to spelling, since there is no justification, except that of conservatism, for the retention of two ways of spelling a suffix which has the same origin and meaning in both terms. The phonographic spelling of 'akene' has long been in use. The usual contractions : T.S. for transverse section, L.S. for longitudinal section, M.V.S. for median vertical section, and so on, have been adopted in the inscriptions.

For help with a number of illustrations I am indebted to some of my past and present pupils, and especially to Mr. F. V. Harvey of Bristol. My thanks are also due to my colleague, Mr. R. D. Went, M.A., for kindly reading through some of the manuscript.

W. Watson.

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CHAPTER I

INTRODUCTION

Some time ago, I was told that a certain naturalist was not a botanist. This statement appeared a strange one as this naturalist was able to name most of our British flowering plants when he saw them growing, and the name of botanist is often applied to a person who has this ability. Botany, however, means much more than the naming of wild flowers ; it embraces a knowledge of the processes by which plants live and reproduce, of the methods by which plants are placed in groups, of the habitats and communities of plants, and some acquaintanceship with their past histories. It must also be noted that botany is not concerned with flowering plants only, but with all forms of life which cannot be placed amongst animals and must therefore include the study of ferns, mosses, sea-weeds, mushrooms, toadstools and other low forms of plant-life.

A botanist cannot expect to have a detailed knowledge of all the different forms of plant-life, and must therefore be content with a general knowledge of the life-histories, structures and methods of life adopted by typical representatives of the different groups. In addition to this general knowledge, the botanist may have a more intimate knowledge of a particular part of the subject. The botanist of to-day is often a specialist in one branch of the subject, and may be relatively ignorant in other branches, though the ignorance must be relative only, or a wrong perspective of the whole subject may ensue. The portion of botany which deals with the naming and grouping of plants is known as systematic botany, that relating to the living actions of plants is called

physiological botany or vegetable physiology, whilst a study of the form or structure of plants is included under vegetable morphology or anatomy. A more intense study of the minute structure of a plant, as it is revealed under the microscope, is called plant histology, and if the cell, which is the unit of life, is specially studied the histologist is then known as a cytologist. Sometimes a particular group of plants is selected for special study, and to a student of each group a distinctive name is given. A student of mosses and plants of near kinship is known as a bryologist, one who studies seaweeds and their allies is an algologist, whilst the study of all the plants which are nearly related to toadstools and mushrooms is termed mycology.

Importance of Field-work. There is only one way in which botany can be studied effectively, and that is to come as closely as possible into contact with the plant as a living body. The student must never get far from nature; the proper place to study the plant is in the field, and all other work must be regarded as supplementary. Detailed dissection of its parts, microscopic examination of its tissues, and experiments on its living activities are often more easily performed in a laboratory, or in a place where the activities may be regulated and controlled, but all the results obtained should be carefully correlated with observations of the plant in the field, otherwise errors due to our artificial manipulation of the plant may creep in.

Methods of Study. There are two entirely different methods of acquiring a knowledge of plant-life. We may begin our study by examining the simplest forms and then working up to the higher and more complicated forms, or we may start with the complex plants, and then work down to the simple ones. We may regard plants as machines, some of which are made up of a large number of parts, whilst others have a very simple and primitive structure. Now, if we want to acquire a sound knowledge of a complicated machine, it is often better to study simpler kinds first, get to know how these work, and then gradually extend our studies till we are able to understand the working of the complicated machine.

This method is the soundest one to follow in botanical work; we ought to examine the minute plants such as Protococcus (the alga which forms a green covering on trees and walls) before we try to unravel the complex machinery of a flowering plant such as the rose. The method, however, has one great disadvantage—we start with plants with which we are not familiar. The flowering plants are much more familiar to us, and we usually begin our work by a careful and methodical consideration of them.

Herbs, Shrubs, Trees. Plants which persist year after year, often for hundreds of years, become woody, and are called trees if they are large, whilst smaller woody plants are known as shrubs. All the other flowering plants are termed herbs whether they possess medicinal virtues or not. To some people a herb means a plant which is used in medicine, and a man who deals in such plants is called a herbalist, but there is no restriction of this kind in the botanical use of the term herb.

Some plants are one-year plants only; they grow from seed, reach their full development, ripen their seeds and die away in the course of a single year. Such plants are called **annuals,** and observations on many of our common weeds will show us that they belong to this group. Other plants do not die down at the end of the first year but persist under normal conditions. If they persist for another year and then die they are two-year plants or **biennials.** The wallflower, turnip and carrot are examples of biennials. During the first year of life they prepare and store up food for their flowering and seed-forming in their second year. When plants persist year after year they are **perennials,** and must have some means of storing food so as to tide them over the winter. Familiar examples of perennials are the potato, which stores its food in underground tubers, mints, which have underground suckers, and trees with bulky tissues, both above and below the surface of the earth.

Selection of Type. For a preliminary survey of the structure of the plant we may take almost any of our common flowering plants, though our selection should not be a

haphazard one. If we desire to study birds we do not select the cuckoo as our type, because it differs from most birds in its method of providing for its young; neither do we take the ostrich as our type since this has practically lost its powers of flight; we take as our type one of our common birds such as the thrush or blackbird which agrees more nearly with the average bird. We must then select for our type of the flowering plants one which agrees in its structure

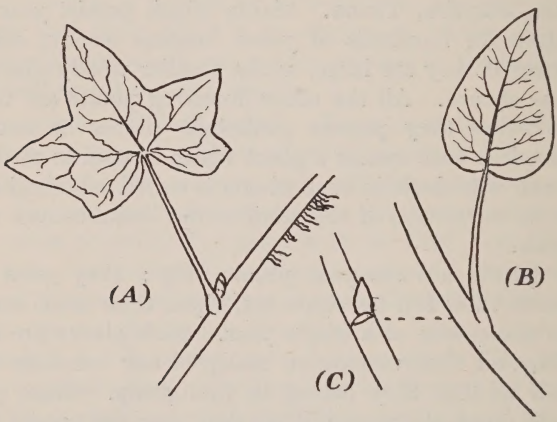

FIG. 1.—Ivy.

A, stem with bud in the axil of a palmately-lobed leaf and adventitious roots. *B*, ovate leaf from flowering-shoot of the same plant. *C*, portion of *B*, showing how the young bud is protected by the leaf-base.

and mode of life with the majority of the flowering plants. The acrid buttercup, which gives such a brilliant yellow colouring to many of our June pastures, is a fair type to take, though many other plants, such as the wallflower, foxglove, shepherd's purse and snapdragon are just as useful. The plant selected must be carefully studied in a practical way, its various parts must be examined, its method of life observed, and as far as possible, its structure should be correlated with its mode of life.

Root, Stem, Leaf. There are three main parts of the

plant, the root which fixes it in the soil, the stem which serves as a supporting structure, and the leaf. The leaf of a flowering plant usually shows little lumps in the angle formed with the stem. This angle is known as the leaf-axil (Fig. 1); the lumps are buds and can be shown to be such by observing their

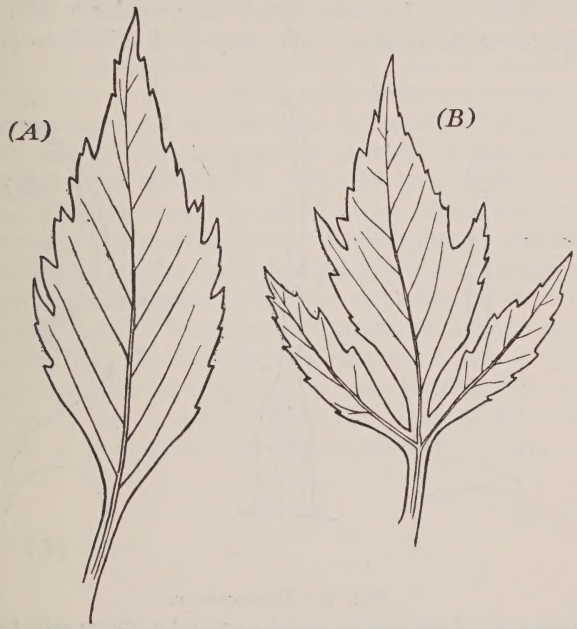

FIG. 2.—Bur-Marigold. Variation of leaves of bur-marigold (*Bidens tripartita*).

A is a lower leaf than *B*. In most plants the more lobed leaves are the lower ones.

development into branches. We may then consider the presence of a bud in the axil as an indication that the body is of the nature of a leaf, and that when a body bears leaves it is a stem-structure, no matter what the shape, size or position of the body is.

In addition, we have bodies which emerge from any of these three parts, e.g. hairs may be present on either the root,

stem or leaf, and we may put all these under a fourth group termed **emergences.** Sometimes emergences become much stronger so as to form prickles (Fig. 3), as in the rose and bramble, and these enable the plant to scramble over other plants. Sometimes the emergences are used for the purpose of reproduction, and it may be advisable to place the latter, which will be dealt with in more detail later, under a fifth group of **reproductive bodies.** We may be inclined to put the

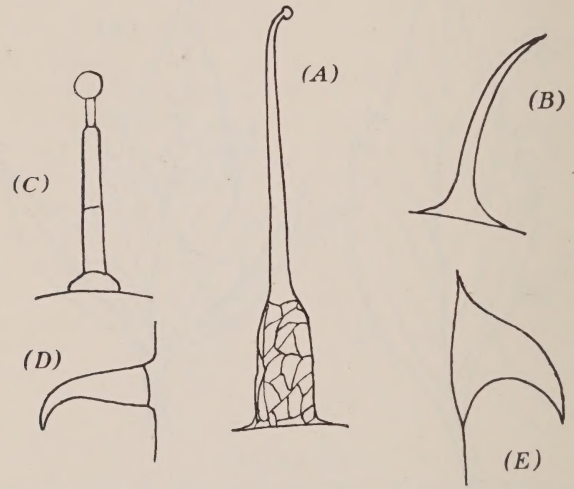

FIG. 3.—Emergences.

A, stinging hair of nettle with a glandular base and a siliceous point (× 50). *B*, ordinary hair from the same plant (× 50). *C*, glandular hair of *Primula sinensis* (× 66). *D*, hooked hair of cleavers (× 66). *E*, prickle of rose (× 2).

flowers under this fifth group, but this inclination must be checked, because it may be possible to regard some parts of the flower as modified leaves. A further consideration of this possibility is postponed to a later chapter.

Correlation of Structure and Function. These different organs or parts of a plant must be studied separately and their characters compared. They must not be treated as dead material, but as living parts doing some particular

work for the plant as a whole. We must find out what the particular work is and how the organ is fitted to do it, therefore we must ask questions of the plant. We endeavour to do so by means of experiments, but it is not always easy to ask a plant the exact question we want answering. The experiment may not always give us the answer we want, but the experiment has not failed; the plant has answered the question put to it, though it may not have answered the question we thought we had put to it. An experiment which is said to fail, is often quite as instructive as one which seems to be successful, if we are able to realize what it actually teaches us. By an experimental method of questioning the plant, it is often difficult to confine the question to one thing; several questions may be asked at the same time and the answer may be a confusing one. In many cases this difficulty can be met by having two experiments set up at the same time, so that the conditions in the two experiments differ in one particular only. The extra experiment is usually spoken of as the control. In the following chapters a number of simple experiments will be suggested to the student, but there are many more which may be tried and some of these may be thought of and considered by the student.

CHAPTER II

THE TWIG AND ITS MARKINGS

During winter the conditions are not favourable for any great display of activity by plants, and therefore we find that many plants during this season appear to be dead or dormant. Some of the small plants are able to fulfil their normal activities, but most plants demand more sunshine and a higher temperature before they can do so. This state of dormancy is most noticeable amongst the larger plants. A few trees and shrubs are evergreen, but the majority are **deciduous**, their leaves having been shed. If we examine a twig of a deciduous tree we note that buds are present, so that on the approach of warmer weather the leaves will be able to appear quickly and the tree display its usual foliage.

One of the best trees to examine during October or November is the horse-chestnut, because the buds are large and the markings are distinct. At the end of the twig there is a terminal bud (Fig. 4), and as this is generally larger than the buds on the side it is usually examined in preference to the lateral buds. We notice that there are some brown scales on the outside arranged in an **imbricate** manner, i.e. something like the slates or tiles on the roof of a house. As these scales are somewhat sticky, it is convenient to have a little methylated spirits handy so that the stickiness can be washed off the fingers. The sticky substance is probably some substance which is of no further use inside the plant and therefore it may be advantageous for it to be removed. If this is so, the exudation of the sticky substance is useful in a double sense ; some waste material is got rid of and then used to bind the scales together. The inner portions of the scaly covering

are greener and inside these some fluffy material is seen. If a piece of this is carefully spread out on a glass slip it is found to consist of five to seven little lobes, and looks so much like a little leaf of the horse-chestnut that we are

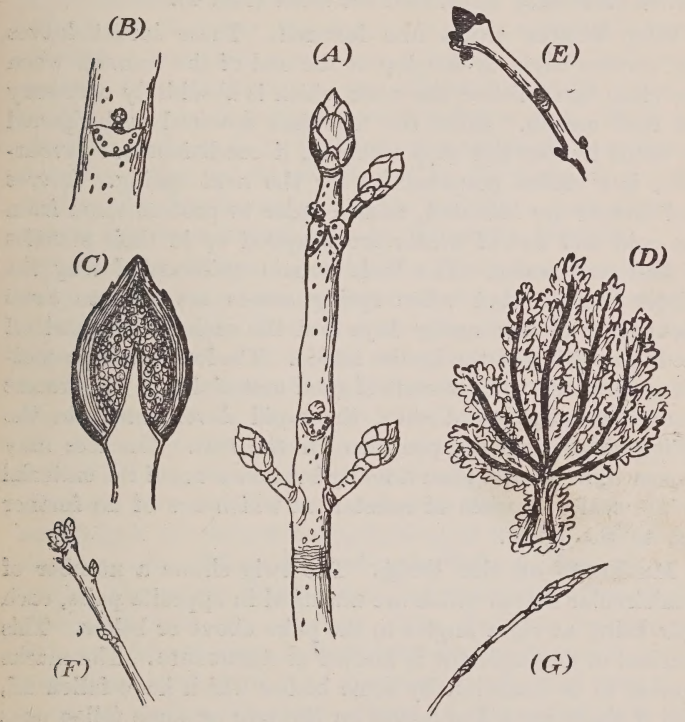

FIG. 4.—Twig and its Markings.

A, branch of horse-chestnut, showing terminal buds, lateral buds, leaf-scars, vein-scars, dormant bud, and lenticels (× ⅔). *B*, small portion of branch (× ¾). *C*, longitudinal section of bud showing axis, flower-buds, crumpled-up leaves, and bud-scales (× ⅔). *D*, infant leaf spread out, and some of the hairs removed from it (× 4). *E*, *F*, *G*, twigs of ash, oak, and beech (× ⅔).

justified in assuming that it is a baby leaf which is protected from drought, mechanical injury or cold by its wrapping of hairs. These hairs are not free from the leaf but are really emergences from it, and are so numerous and relatively long

that they appear to enclose the leaf in a cottony cocoon. In some of the larger buds we also find little brownish grains, and these are flower-buds. Finally, right in the centre of the bud, we find the **axis** or young stem, and on this all the bodies previously mentioned are fixed (Fig. 4).

Why Winter Buds are formed. These infant leaves and flowers begin to develop at the end of the summer when the plant has finished the work which is absolutely necessary for that season. After the tree has flowered and ripened its seeds it does not stop working, if conditions are favourable, but makes preparations for the next spring. Leaves and flowers are initiated, and in order to protect them from the cold and wet of winter are wrapped up in their mantles of hair and scales. The buds remain quiescent during the winter months, but when spring comes are able to avail themselves of any sunny days and the scales are forced off by the swelling of the bodies inside. The loss of the protective scales seems to be a waste of good material, but the process is economically sound since the rapid development in the spring more than compensates for the loss. The loss may appear to be greater than it really is, since some of the material in the scales consists of substances which are of no further use to the plant.

Markings on the Twig. The twig shows a number of semicircular marks which are arranged in opposite pairs, each pair being at right angles to the pairs above or below. This method of arrangement is known as **decussate.** The marks appear to be scars left by some bodies which have fallen off, and if there are a few leaves on the tree or some fallen ones lying on the ground we can easily convince ourselves that the marks are **leaf-scars,** since the base of a leaf-stalk fits a scar. On the leaf-scar from five to seven smaller marks similar to the nails in a horse-shoe are present and these must be the scars of the veins which passed into the leaf-lobes.

Leaf-fall. The leaves are said to fall off, but it is more correct to say that they are pushed off. When a large branch is broken at the end of summer the leaves on that branch wither, but they do not come off in the same way as the

leaves from uninjured branches, so that it seems as if the tree makes preparations for the shedding of its leaves (**defoliation**). The process of defoliation varies in different trees, but usually a separation layer of large and thin-walled cells is formed across the base of the leaf-stalk. The walls of these cells partly disappear and then some corky material is formed beneath. Any further passage of water to the leaf is prevented, the leaf dries up, and alterations in its contained substances give the characteristic autumn tint. It is then attached to the twig by the dried-up remains of the separating layer, and the weight of the leaf or the force of the wind renders the detachment complete, leaving a scar where the wound has been healed over by the corky material.

Bud-Scale Scars. Besides the horse-shoe markings, the twig shows some closely-crowded ring-like markings. A careful examination shows that the rings do not go completely round the stem but that their deceptive appearance is due to a number of narrow scars which are closely crowded together. These scars must be due to the fall of a large number of bodies about the same time, and as this occurs when the bud-scales fall off we may assume that these apparent rings are due to bud-scale scars. This assumption may be made into a certainty if we observe the unfolding of the buds when April comes round. When the bud-scales fall off, the axis of the bud is elongating slightly and the scars are often slightly separated from one another. The distance between two different lots of rings is that between the terminal buds of two consecutive years, and therefore shows what growth has occurred during the year. Some of these bud-scale scars show vein-scars, and above some of them little buds are seen, therefore the bud-scales must be modified leaves, or, at any rate, leaf-bases. Usually they fall off when the bud opens out, but sometimes an odd one may be found which has developed a leaf-blade, thus confirming our theory. This occurs very seldom in the horse-chestnut, but is often found in the maple (Fig. 5), and may be induced artificially by cutting off the proper leaves.

Dormant Buds. Buds do not always show above the

bud-scale scars, but this does not interfere with our theory that the bud-scales are modified leaf-bases, since we do not always find a bud showing in the axil of an ordinary leaf, and in many cases the bud is small. The buds which do not develop normally are called dormant buds, and may often be induced to proceed with their growth by cutting off the parts above them. In an ordinary hedge, the buds which are most favourably situated in regard to light or any other influence will be the best-developed, and a hedge which is allowed to grow naturally becomes straggling and untidy.

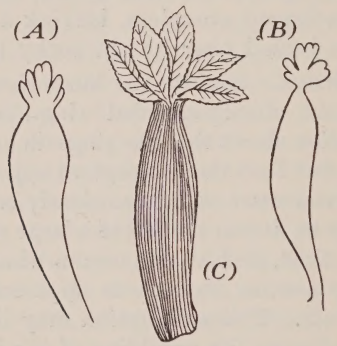

Fig. 5.—Bud-scales developing into Leaves.
A, *B*, maple (April). *C*, horse-chestnut (May).

The hedgecutter's constant attention causes a more even development of the buds, more buds proceed to form branches and the hedge becomes thicker.

Lenticels. On our twig we can also find little brown dots which are called lenticels (Fig. 4) and are for the purpose of allowing gases to enter or leave the stem. During summer the lenticels are paler in colour than they are in winter, because during the latter season less interchange of gases with the atmosphere is taking place, and the lenticels are covered over with a thin layer of cork (Fig. 102).

Galls. On our horse-chestnut twig we may find little red lumps which are due to a fungus (*Tubercularia*) though these

are rare on a living twig, but if we examine the twigs of the oak we often find brown spherical bodies about the size of a marble. These are known as galls (Fig. 6) and are initiated

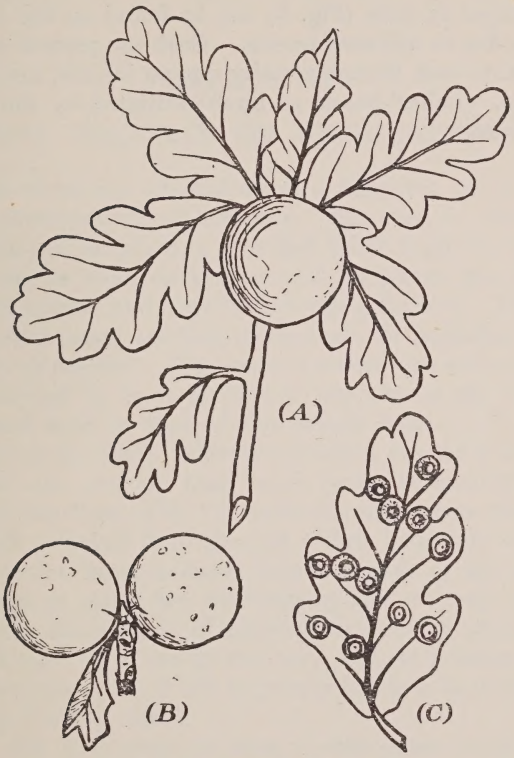

FIG. 6.—Galls of Oak.

A, oak-apple, due to the attacks of a wasp. *B*, gall formed by *Cynips* (December). The hole through which the insect escaped is shown in the gall on the left-hand side. *C*, spangle-galls due to a minute wasp.

by an insect laying an egg in the tissues of a leaf or twig. The injury to the cells stimulates growth, so that the injury may be repaired. When the egg becomes a grub the plant-material is used as food, and so the gall becomes larger as

further attempts to cope with the ravages of the insect are made. In the common spherical oak-gall the grub can easily be found when the gall is juicy, whilst in a dried-up gall the hole through which the insect escaped can be seen (Fig. 6, *B*). Other shapes of galls (Fig. 6) can be found on the oak, and these are due to different insects. Galls are present on many other plants and, though usually due to insects, are in some cases (e.g. witches'-broom of birch) initiated by the attacks of a fungus.

CHAPTER III

THE SEED AND ITS GERMINATION

To most of us, the life-history of a flowering plant begins with the development of the seed. The seed is planted in the ground and moisture is provided till it begins to sprout, then we see its stem elongating and its leaves growing till the flowers appear and seed is once again formed. The seed then is a convenient starting point in an investigation of the life-history of a plant. The seeds of buttercups are too small to be examined by us at present, so we take as our example a large seed such as that of the kidney bean.

On soaking the seeds in water for about twenty-four hours they swell out, and are then much easier to examine. On one end of the bean (Fig. 7), we find a scar where the short broad stalk attached it to the pod. Just below the scar, on one side of the bean, a small hole is visible in the skin or **testa.** This is called the **micropyle,** and we may imagine that it is for the purpose of allowing the seed to sprout, and perhaps it may be of use in this way, but its primary use is a very different one and will be referred to in a later chapter. (See Chap. XIV, p. 130.)

Below this hole may be seen a triangular body which shows quite clearly on taking off the testa. It appears to be a little sprout fastened to two large bodies. On opening out the large bodies we find some little thin bodies at the other end of the sprout-like organ, and on examining them with a magnifying glass they are revealed as miniature leaves. The portion on which the leaves are fixed must be a stem, and therefore the triangular portion at the other end is a baby root. The seed is therefore a miniature plant, enclosed in a

case which protects it and prevents it from developing before a suitable time. The infant root is known as the **radicle,** whilst the baby shoot is called the **plumule.** The two large bodies, which are called **cotyledons,** form such a large portion of the seed that they must have some important work to do, and we may infer that they contain some food substance on which the embryo plant can feed before it is able to obtain food from other sources. This can be shown to be true by watching the development of a bean plant and noticing the shrinkage of the cotyledons as the plant grows larger (Fig. 7).

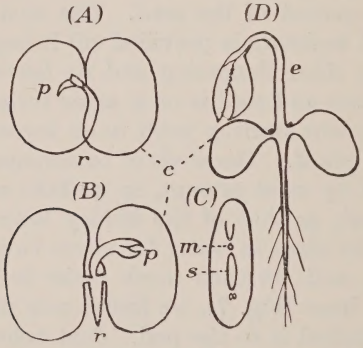

FIG. 7.—Seed of the Kidney-bean and its Germination.

A, *B*, soaked seeds with the cotyledons spread out to show the radicle and plumule. *B*, is somewhat diagrammatic so as to indicate that the cotyledons are modified leaves. *C*, side-view showing micropyle, position of the radicle and scar of attachment to the pod. *D*, young bean plant. In the axils of the cotyledons, buds are developing. *c*, cotyledons; *e*, epicotyl; *m*, micropyle; *p*, plumule; *r*, radicle; *s*, scar.

On putting the scrapings from the surface of a cotyledon on a white dish, and adding a drop of iodine, a blue coloration is produced, and as this is the reaction for starch, it shows that the baby food contains this substance. If we put a thin scraping in a drop of water, and examine it under a low power of the microscope, we find that it consists of a number of packets, or cells as they are called, and these are full of little grains which turn blue when iodine is added.

On examining very carefully, we find that the cotyledons are attached by short stalks to the plumule (Fig. 7) and if

they were much smaller and thinner we should have little hesitation in referring them to leaves. They occupy the same positions as leaves, and sometimes buds are developed in their axils (Fig. 7, *D*), so that we must conclude that they represent the first leaves of the bean plant, and have become enlarged and thickened in order to provide a store-house of such food as the baby plant is able to live upon.

Hypogeal and Epigeal Plants. In the bean, pea and many other large-seeded plants, these cotyledons remain below the surface of the ground, but in many plants the store of food is insufficient and so the cotyledons are forced above the ground, becoming green and actually functioning as the first green leaves of the plant (Fig. 8). When we grow mustard and cress for the table the bodies which are eaten are the green cotyledons; the real leaves appear later, and are borne on the plumule which grows between the cotyledons. In these seedlings the portion of the stem below the cotyledons is rather long and is known as the **hypocotyl** (Fig. 8). Those plants in which the cotyledons remain below the surface of the earth are said to be hypogeal, whilst those whose cotyledons grow up to form the first green leaves of the plant are epigeal.

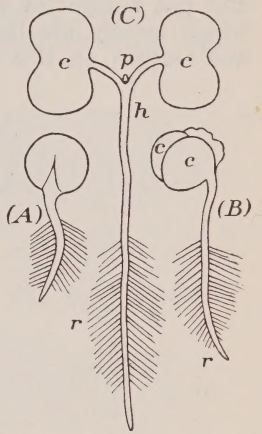

FIG. 8.—Germination of the Mustard.

A, testa split and radicle formed. *B*, cotyledons emerged, the testa being pushed to one side. *C*, older seedlings in which the cotyledons have opened out and the plumule has appeared. *c*, cotyledons; *h*, hypocotyl; *p*, plumule; *r*, radicle with root-hairs (note that no root-hairs are present at root-tip).

The following experiments should be performed by the student.

EXPERIMENT 1. To show the germination of peas. Immerse some sawdust in a bucket of water and stir till it becomes thoroughly wet. Put a layer of wet sawdust, 4 or 5 inches thick, in a box, and sow some peas in it,

keeping them at least an inch apart and about half an inch deep. Pull up one or two every day, note what has happened and make drawings.

EXPERIMENT 2. To grow a bean in a damp chamber. Take a bottle about 2 to 3 inches in diameter and with a wide mouth. Place blotting-paper round the sides of the bottle, except for a vertical strip of about an inch in width, and put a layer of water at the bottom. Through a cork which loosely fits the mouth of the bottle pass a hat-pin and impale on it a soaked bean, taking care that the pin

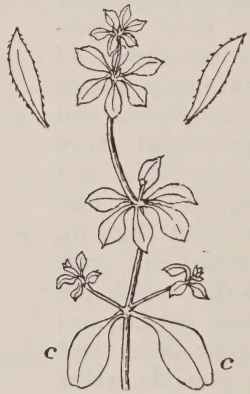

FIG. 9.—Juvenile condition of Cleavers.

Cotyledons (*c*) are still present, and the leaves have not assumed their adult form. Two of the adult leaves are shown at the sides.

passes through the cotyledons. Place the cork in the bottle so that the bean is over an inch above the level of the water. Observe the changes which occur and make notes and drawings.

EXPERIMENT 3. To show the germination of mustard and cress. Take a shallow wooden box, place two sheets of blotting-paper on the bottom, and on this place a little dish containing water. Place a strip of blotting-paper so that one end is in the water and the other on the bottom of the box. Wet the blotting-paper, and sow mustard on one half and cress on the other. Examine from time to time, at least once every twenty-four hours, and make notes and drawings.

Compare the growths of the mustard and cress, and also compare with the results of the previous experiments.

EXPERIMENT 4. To show the germination of a monocotyledon. Proceed as in Expt. 1, except that soaked grains of wheat or barley are used in place of peas.

EXPERIMENT 5. To show the zone of maximum growth in a root. Prepare a damp chamber as in Expt. 2. Take some soaked and germinating beans, pin them to a piece of cork and mark the radicles with lines in Indian ink 1 mm. apart,

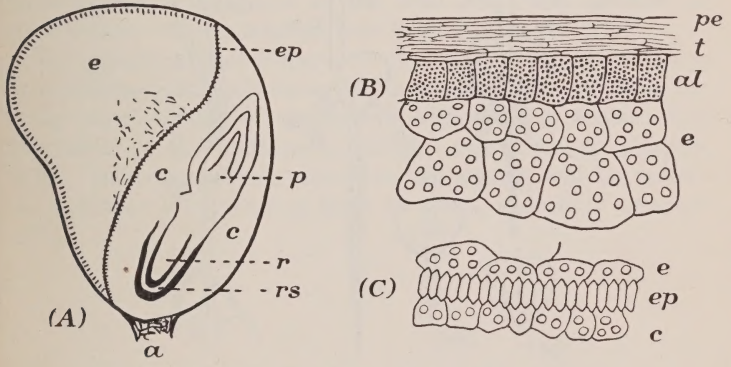

FIG. 10.—Grain of Maize.

A (× 5), longitudinal section, cutting through radicle and plumule. *B* (×250), L.S. of outer portion. *C* (× 250), L.S. through epithelial layer and adjoining cells; *a* attachment to cob; *al*, aleurone layer; *c*, cotyledon; *e*, endosperm; *ep*, epithelial layer; *pe*, pericarp; *p*, plumule; *r*, radicle; *rs*, root-sheath; *t*, testa. In *A* the endosperm adjacent to the epithelial layer is indicated as being altered by the ferment from the cells of that layer. In *B* and *C* starch grains are shown. In *B* aleurone grains also are indicated.

beginning from the tip. Wedge the cork in the glass jar or attach it to the cork stopper and keep in the dark. Note that little growth occurs at the root-tip and that the zone of maximum growth is about the 4th or 5th one from the tip.

EXPERIMENT 6. To show the zone of maximum growth in a stem. In a similar way as in above expt., fit up an apparatus in which well-developed hypocotyls of mustard or sunflower seedlings are marked in zones and tabulate the results. Note that growth occurs in all the zones and that the greatest growth occurs about the 9th zone from the top of the hypocotyl.

Monocotyledons and Dicotyledons. The development of seedlings can also be observed in the field; seedlings of cleavers (Fig. 9) are very common in many hedgerows during mild winters, and the cotyledons of beech should be searched for. Most of our common flowering plants have two cotyledons in their seeds, and are therefore called Dicotyledons, but there are many plants in which the seed contains one

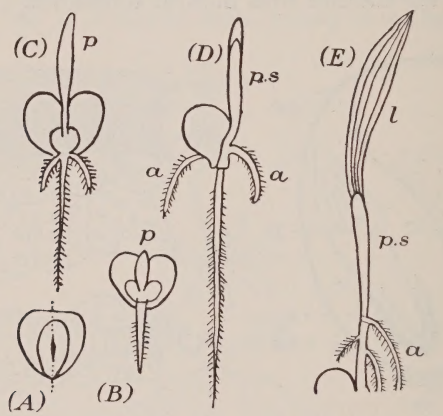

FIG. 11.—Maize and its Germination.

A, grain in surface view, showing scutellum and positions of radicle and plumule (the dotted line represents the line along which the section shown in Fig. 10 was taken). *B*, *C*, *D*, *E*, stages in the development of seedling (somewhat diagrammatic): *B*, *C*, front view; *D*, *E*, side view. *a*, adventitious roots; *l*, leaf; *p*, plumule; *ps*, plumular sheath.

cotyledon only, and these are known as Monocotyledons. The lily, tulip, hyacinth, daffodil, wheat, barley and the grasses are monocotyledons, in fact, most plants having similar leaves to the above-mentioned plants have only one cotyledon in the seed.

The seed of a monocotyledon should be examined, and its structure compared with that of a dicotyledon, but its dissection is not so simple as in the bean. Grains of maize (Fig. 10) may be taken, softened by soaking in hot water, and pulled to pieces, but a better method is to cut longitudinal sections. At the more pointed end of the grain,

the scar of its attachment to the cob can be seen, and one of its flat sides shows a little shield or **scutellum** (Fig. 11). The section should be made so as to divide the scutellum into two equal parts, and then the radicle and plumule will be revealed as shown in Fig. 10. The scutellum is really the single cotyledon, and the grain contains, in addition to the embryo, a large amount of food-material which is known as **endosperm.** It must also be noted that the grain is not only the seed but the seed-pod as well, and that the testa is closely adherent to the seed-pod. The method of germination in a monocotyledon is shown in Fig. 11.

The presence of endosperm in the seed must not be taken as a distinguishing character of monocotyledons as there are many dicotyledons which possess endospermic seeds. The formation of the endosperm will be considered in Chapter XIV. Other structures shown in the figures will be understood better after reading later chapters, especially Chapter XIV.

CHAPTER IV

THE ROOT AND ITS MODIFICATIONS

The baby root, or radicle, as we have seen, is present in the seed. It is usually the first part of the embryo plant to emerge from the seed, and its further development varies in different plants. If this primary root elongates and gets thicker, it is said to be a persistent primary root or **tap** root, but when the primary root branches very quickly a root

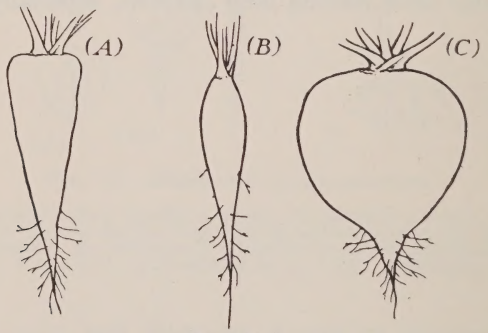

FIG. 12.

A, conical root of carrot. *B*, fusiform root of radish. *C*, napiform root of turnip.

system consisting of a number of branches is formed. These branched roots may consist of slender threads, as in the **fibrous** root of a grass or sedge (Fig. 22), or some of the branches may swell out to form **tuberous** roots, as in the dahlia (Fig. 13) or lesser celandine (Fig. 31). The most common kind of tap root is **conical** (Fig. 12), as in the carrot and parsnip, whilst other familiar forms are the **napiform** root of the turnip (Fig. 12) which is very much swollen in

the middle, and the **fusiform** root of the radish (Fig. 12) which is somewhat swollen in the middle and tapering at both ends. In all these cases, the thickened roots serve as storehouses of food reserved for feeding the plant when it is doing a lot of work such as forming flowers. The first, main or **primary** root is also called a root of the first order, whilst the branches from this are lateral roots. The lateral roots which appear on the primary root are roots of the second order or **secondary** roots, and if branches appear on these they are known as roots of the third order or **tertiary** roots.

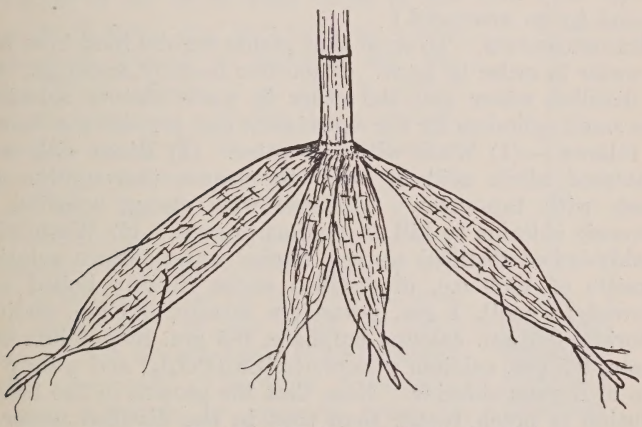

FIG. 13.—Branched Tuberous Root of Dahlia.

The following experiments should be performed before the further consideration of the root.

EXPERIMENT 7. To show that water is absorbed by the plant. Take two test-tubes, and fit with corks through which holes have been bored. Cut each of the corks lengthways, so as to divide into two similar halves. Pack a small plant with cotton-wool between the two halves of one cork, fit into a test tube containing water, and mark the level of the water with a strip of stamp-edging. The plant must have its roots intact, therefore the soil must not be roughly shaken from them, in fact, it is advisable to keep the plant after it has been pulled up for a few days in water so as to allow it to recover

from any injury to the roots. Fit up the other test-tube (as a control) in an exactly similar way, except that no plant is present. Note any alteration in the levels of the water in the two tubes, that in the control being due to ordinary evaporation.

Experiment 8. To show the effect of root-hairs on the absorption of water. Proceed as in the last experiment, except that small plants are fitted into both tubes and that one plant has had the soil shaken roughly from it in order to remove the root-hairs. (It is difficult to set this question properly to the plant : the results of the experiment are often very instructive, though they may not be direct answers to the question intended to be answered.)

Experiment 9. To show that plants require food from soil or water in order to grow. Place two healthy seedlings, one in distilled water and the other in water-culture solution. Use small cylinders for the experiment and prepare the vessels as follows :—(1) Wash with tap-water. (2) Rinse with concentrated nitric acid in order to cleanse thoroughly. (3) Wash with tap-water. (4) Rinse with strong solution of mercuric chloride to kill any germs present. (5) Wash with freshly-boiled distilled water. Sachs' water-culture solution consists of 1000 c.c. of distilled water (freshly boiled and allowed to cool), 1 gm. potassium nitrate, 0·5 gm. sodium chloride, 0·5 gm. calcium sulphate, 0·5 gm. magnesium sulphate, 0·5 gm. calcium phosphate [$Ca_3(PO_4)_2$] and a drop or two of ferrous chloride. Note that the growth in the Sachs' solution is much better than that in the distilled water.

Experiment 10. To show that substances must be in solution in order to be taken up by the root-hairs. Obtain two uninjured plants, place one in water containing eosin dissolved in it, and place the other in water containing undissolved carmine. Use boiling tubes or small cylinders for the vessels containing the plants, and add a little Sachs' solution to the water. Note that the plant in the tube containing the eosin solution becomes coloured, whilst that in the other tube does not. The poisonous action of eosin, when the plant is left for some time, may also be noted.

Experiment 11. To show that roots elongate in order to reach the nutrient solution. Fit up a plant in a test-tube containing Sachs' solution, by means of a split and bored cork as in Expt. 7, and allow it to remain for several weeks. Have

a control experiment, where the plant is kept well supplied with water, also going on. (This experiment may give results requiring careful interpretation.)

Experiment 12. To illustrate the process of osmosis. Tie a piece of moist pig's bladder to the mouth of a thistle funnel (Fig. 14). Fill the vessel so formed with a strong solution of copper sulphate. Invert the funnel in a cylinder of distilled water, fix on a stand and mark the level of the copper sulphate in the stem of the funnel.

Osmosis. In the above experiment the blue solution of copper sulphate in the stem of the funnel rises owing to the passage of water into the solution. This passage is known as osmosis, and the force which causes it to rise is called osmotic pressure. If left long enough the blue colour of the water in the jar shows that copper sulphate has passed from the funnel, so that eventually equilibrium will be established, the concentration of the solution in the jar will be the same as that in the funnel, and the levels will be the same in both vessels. The experiment may be repeated with a solution of another substance, such as saltpetre, or sugar, in order to show that it takes place with other soluble salts or substances. Any salt soluble in water has a similar action, and there must be some physical process going on which forces water through the membrane. What this process of osmosis really is does not necessarily concern us here, so long as we know that there is such a process, and that it acts so that water, and substances dissolved in it, can pass through a suitable membrane. In our germination experiment with the mustard (Expt. 3) a number of white hairs (Fig. 8) were seen on the sides of the radicle. These root-hairs are the chief agents in the absorption of water, their walls act as suitable membranes for osmosis to occur, and water is passed from the soil into the root.

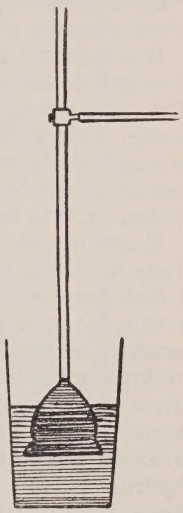

Fig. 14.— Apparatus for showing Osmosis.

Experiment 13. To show the positive geotropism of a root and the negative geotropism [1] of a shoot. Fix some germinating peas (with plumules about half-inch long) by means of pins on a sheet of cork so that the radicles and plumules are horizontal or almost so. Fix the sheet of cork tightly in a glass jar containing water at the bottom and cover with a bell jar or insert a loosely-fitting cork. Place the apparatus in the dark, so that any effects produced are not due to light. Place a similar apparatus in the light. Note how the radicles curve towards the earth whilst the plumules curve upwards.

Experiment 14. To show that the radicle does not grow downwards because of its weight. Place some mercury in a dish with a wooden bottom, and cover it with a thin layer of water. Fix a young pea seedling horizontally by passing a pin through the cotyledons and insert the pin into the wooden bottom of the box so that the seedling is above the level of the water. Cover with a bell jar, and keep in the dark.

Experiment 15. To show the hydrotropism [1] of roots. Take a wooden box (about 12 inches long, 7 inches broad, and 1 inch deep) with a zinc gauze bottom. Cover the gauze with a thin layer of moist soil or sawdust, and in this sow some mustard seeds. Suspend the box so that its bottom makes an oblique angle with the vertical. Keep in a cupboard, adding a little water if necessary. Support another apparatus in a horizontal manner. In this experiment the roots are attracted towards the earth by geotropism, and towards the water by hydrotropism. The behaviour of the radicles after they have penetrated through the holes of the wire gauze will depend upon the relative strengths of the two influences. If hydrotropism is stronger than geotropism, the radicles will grow towards the water.

Experiment 16. To show the root-pressure in a plant. Fit up the apparatus shown in Fig. 15 (description of parts of apparatus in inscription). *M* is a glass tube to act as a manometer, i.e. to measure the pressure, mercury being placed in it to the level *x*, *x*. A vine is one of the best plants to experiment with during spring-time. In summer a Eupatorium or Fuchsia plant may be used. Fit the T-tube with three pieces of pressure tubing at *a*, *b* and *c*, wire the joints, and plaster with surgical bandage. Cut off the stem of the plant at *b*

[1] See p. 28.

under water, fit the pressure tubing on, wire and plaster. Attach the manometer at *a* whilst the whole apparatus is under water, so that no air-bubbles are present. Wire and plaster the joints at *a*, and clamp at *c*. Take readings of heights of barometer and thermometer, and note the rise of the mercury in the tube *M*. The difference of level in the two arms of the manometer *M* (corrected for atmospheric pressure and temperature) will show the root-pressure. Water passes by osmosis into the cells of the roots, is given off by the cut end of the stem, and causes the level of the mercury to rise.

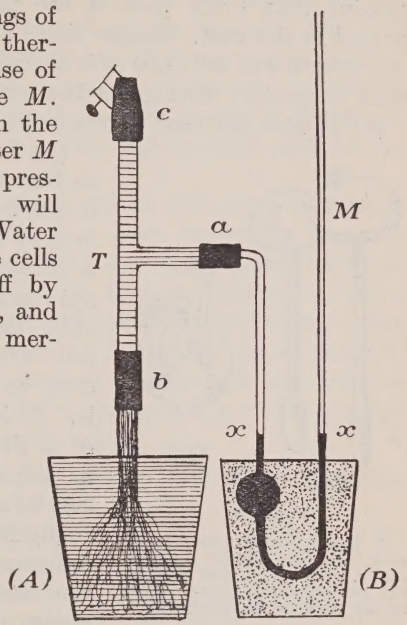

FIG. 15.—Diagram of Apparatus for showing Root-pressure.

A, plant-pot filled with soil. *B*, plant-pot filled with sawdust. *T*, T-tube filled with water; *M*, manometer with mercury to the level *x*, *x*. *a*, *b*, *c*, rubber (pressure-tubing) joints wire dand plastered; the free end of the rubber at *c* is closed by a clamp.

Functions of the Root. The two primary uses of the root are to fix the plant in the ground and to get water and food from the soil, the food, as we have seen from our experiments, being dissolved in a large quantity of water. The minute root-hairs (Fig. 8), which are so well shown when the mustard is grown on blotting-paper, are very useful for both these purposes, especially for the supply of water and the substances dissolved in it. The countless root-hairs are so closely adherent to the particles of soil that they easily break off when the plant is pulled up. It is this close attachment of the root-hairs to the soil which renders transplanting difficult, so many of the absorbing hairs are broken off that the

plant is unable to obtain water sufficient for its needs and it therefore wilts or flags and may die away.

Distinguishing Characters of the Root. We must not imagine that every part of the plant which is below the ground is the root, because there are many stem structures underneath the soil, and it is therefore necessary to consider what characters distinguish the root from the stem.

(1) It does not bear leaves or buds.

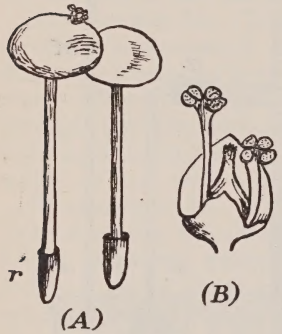

FIG. 16.

A, Two Plants of Lesser Duckweed (× 5), one of which is flowering. *r*, root-cap. *B*, One pistillate and two staminate flowers in unequally lobed spathes (× about 25).

(2) It has its apex thickened, so that the actual growing-point is not at the end, but is covered over by layers of cells which form a root-cap. This root-cap does not bear any hairs, and it enables the root to bore into the soil without any injury being done to the delicate cells above it. It is well shown on the roots of a little floating plant known as the duckweed (Fig. 16), and can be seen by the use of a lens.[1]

(3) It is sensitive to external influences in a different way to the stem; it turns towards the centre of the earth (Expt. 13), towards water (Expt. 15) and away from light. These three responses to stimuli are called tropisms, and suitable prefixes are used to distinguish between the different kinds. The directive influence of the earth is known as **geotropism**, and as the root turns towards the earth it is said to be positively geotropic. The directive influence of water is called **hydrotropism**, and the root is positively hydrotropic. The reaction to light is of an opposing nature, and the root is said to show negative **heliotropism**.

(4) A branch root has an **endogenous** origin, i.e. its first

[1] The cap-like covering on the end of a duckweed root is considered to be rather different from a root-cap, since tissues of the root-sheath take part in its formation.

indication is a little group of cells inside the older root. As this little group of cells gets bigger, the outside of the older root bulges, and the young root forces its way out, in fact it may almost be said to "eat its way out," as the cells which are obstructing its passage to the soil are disorganized (Fig. 107).

(5) The internal microscopic structure of a root is characteristic. If a thin slice or section of a root is examined under a microscope, it is usually an easy matter to distinguish it from a section of a stem. This will be dealt with further in Chapter XVI.

(6) Lateral roots are given off in acropetal succession. During the normal growth of a root, branching does not occur in a haphazard manner, but the lateral roots are produced in a regular order, so that the youngest root is nearest to the root-tip, and the oldest furthest away. This order or succession is known as **acropetal** (*acer*, summit; *peto*, seek). This regular order of branching is also followed in the stem, so that it is not a character by which the root can be distinguished from the stem.

Adventitious Roots. The normal method of branching often seems to be departed from, especially in monocotyledons (Fig. 11), and the roots are then known as adventitious, as their advents or appearances are out of the normal order or position. It is well known that a stem can be induced to form roots on it, and such roots must be adventitious. The roots which attach the ivy to the tree or wall are examples of adventitious roots which may be some distance above the ground, and these roots are said to be **aerial** adventitious roots (Fig. 1). They have been modified to form tendrils which enable the plant to climb, but their correspondence (homology) to roots is shown by their ability to form true

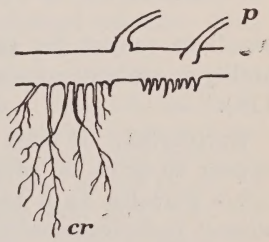

FIG. 17.—Adventitious Aerial Roots of Ivy.

At *cr*, penetrating into the crack of the wall containing soil, and forming actual roots; *p*, petiole of leaf (lamina not shown).

roots when they come in contact with the soil. A little search on an old ivy-covered wall will probably reveal crevices where soil is present and in which the tendrils elongate and form real roots (Fig. 17). The adventitious roots of the ivy-leaved toadflax are very near the surface of the soil in the crevice of the wall, and are said to be **subaerial**. The aerial adventitious roots of some trees, as the banyan and mangrove, are very large.

Parasites. There are some plants which do not send their roots into the soil, but draw their nourishment from another plant, and these plants are called parasites. A familiar parasite (at least in part) is the mistletoe which grows on many kinds of trees, and especially on the poplar and apple. The parasitic roots (**haustoria**) can be traced as greenish portions (Fig. 18) in the wood of its host. The dodder, which grows on gorse and ling, is also an excellent subject for the study of haustoria, though some ability in making microscopic preparations is necessary (Fig. 118).

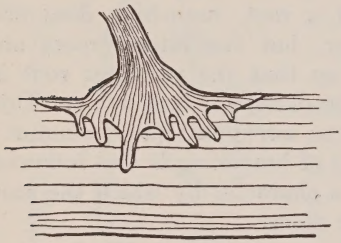

FIG. 18.—Parasitic Roots (Haustoria) of Mistletoe.

Epiphytes. It must not be inferred that all plants which appear to grow on other plants are parasites. The ivy is not a parasite, as it has its own roots in the ground, from whence it derives nourishment. The common polypody often ornaments the depressions between the branches of a tree, but it is not a parasite, since its roots are growing into a little soil which has found lodgment in the depression. The lichens (Chap. XXXI, Figs. 122 and 220), which drape or mantle the bark of many of our trees with their varied tints of greys and yellows, are not parasites, since they do not rob the tree of food, but obtain their requisite water and mineral food from the liquid which trickles down the bark. All such plants which grow on other plants are styled epiphytes.

CHAPTER V

THE STEM AND ITS MODIFICATIONS

The stem is developed from the plumule, which, as the seedling enlarges, forms a shoot consisting of the primary stem and leaves. At the apex of the stem there is a growing point, which is continually adding new cells, and this is covered over by young leaves. As these young leaves are initiated below the growing point of the stem, they must have grown more quickly than the stem in order to overtop it. Owing to this precocious growth, the delicate young cells of the growing point are protected by the overlapping leaves.

EXPERIMENT 17. To show that water passes up the stalk of a plant. Place a white flower, such as the snowdrop or narcissus, with its stalk dipping into diluted red ink. Note the coloration and the marking of the petals.

EXPERIMENT 18. To show that water passes through the plant by means of the wood and veins. Make two incisions, about 2 mm. apart, around the bark of a woody stem, and peel off the bark so as to leave a ring of wood bare (this operation is known as ringing). Place the lower end of the branch in diluted red ink, leave for a few hours, and then note the coloration of the leaves above the ring. Make a transverse cut across the stem and note that the pith is uncoloured, therefore the coloured water must have travelled through the wood. Branches of privet, cherry-laurel, or willow are suitable for this experiment. The coloration of the veins of the petals in the previous experiment showed that the coloured water passes along the veins.

EXPERIMENT 19. To show the negative geotropism of stems. In a zinc box (about 24 × 12 × 12 inches) with a tightly fitting lid, place moistened sand, so that it slopes

from one end to the middle of the box at an angle of about 50°. Fix grass haulms, with nodes on them, horizontally in the wet sand. Close the lid so that the influence of light is eliminated, and observe during the next day how the haulms have become bent upwards at the joints or nodes. Haulms of grasses are stems with sheathing leaves fastened to them at the nodes where actively-growing tissue is present.

Experiment 20. To show the positive heliotropism of a shoot. Place moist sawdust in a plant-pot, and grow some mustard seed on it. Remove the young seedlings to a dark room, and allow them to grow till they become erect and about $1\frac{1}{2}$ inches high. A little soil or food solution may be added to the sawdust. Place the pot in a heliotropic chamber with the slit near a window, and observe how the plants curve towards the slit. A heliotropic chamber is a box blackened on the inside and " light-tight " except for a slit on one side.

The seedlings will also be affected by geotropism. The effects of geotropism may be eliminated by means of a clockwork arrangement, so that either the whole chamber or the plant-pot inside is slowly turned. The plant-pot must be placed horizontally so that geotropism acts regularly on all sides of the plant, and suitable accommodations for preventing the sawdust from falling out, etc., must be made.

Functions of the Stem. The two chief uses of the stem are to support the leaves and flowers, and to convey food-substances to different parts of the plant, but they may also serve for some subsidiary purpose. They may help the root to fix the plant or may assist the leaves in their work, or may serve as storehouses of reserve food.

Distinguishing Characters of Stem.

(1) It bears leaves or buds. In an underground stem the leaves are often reduced to brown scaly bodies, and sometimes merely the leaf-scars are visible.

(2) Its growing point is not protected by a cap of tissue, as in the root, but is covered over by the young leaves forming a bud.

(3) It is usually negatively geotropic and positively heliotropic. Positive heliotropism is usually well shown by window plants, most people being familiar with the way in

which geranium (*Pelargonium*) plants turn towards the light. The hydrotropism is usually not pronounced, but is generally opposite to that of the root.

(4) A branch from the stem has an **exogenous** origin, i.e. the group of little cells, which gives rise to the branch, appears as a little bump on the outside of the stem.

(5) Its internal microscopic structure is characteristic (see Chapter XV).

(6) The normal method of development is, like that of the root, one of acropetal succession.

Adventitious Shoots. As in the root, the normal method of branching is often departed from, and adventitious shoots are formed. A plant may be stimulated to produce adventitious shoots artificially on almost any of its parts. A common method by which they are produced is that known as **pollarding**. Many trees which adorn our streets would become too large and straggling if allowed to grow in their own way, so their branches are lopped off every year, new growing points are initiated, and a number of branches grow from the wound of the preceding season. The basket-makers exploit this ability of the plant to produce fresh-growing

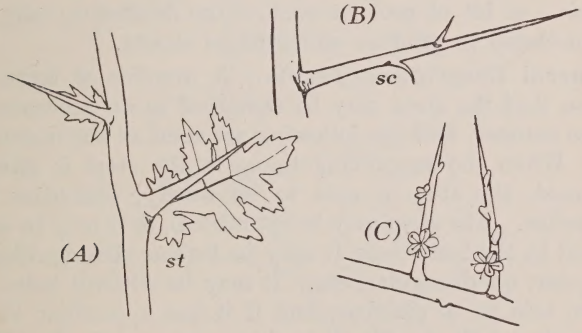

FIG. 19.—Stem-Spines.

A, hawthorn. Note that the spine is in the axil of the stipulate and lobed leaf, showing that it is a modified branch. *B*, spine of hawthorn with secondary spines. The leaves have fallen off but the scars show that the spines were formed in the axils of leaves. *C*, spines of sloe, bearing flowers and buds. *sc*, leaf-scars; *st*, stipules.

points. They cut off the branches of the willow, and from the cut surfaces arise many branches which are sufficiently slender for weaving into baskets.

Adventitious shoots occasionally form on stumps which have been put into the ground before they have "seasoned" properly. In some cases, the shoots may not be really adventitious, but may be deferred ones, which have arisen from dormant buds. On some trees, especially birch, a bundle of small twigs may often be seen. These peculiar structures were formerly attributed to witches, and were familiarly known as witches' brooms. Their method of formation is similar to that of the adventitious shoots in pollarded willows, but the injury which stimulates the plant to form new buds is not due to a human agent, but to the attacks of a fungus. A gardener often produces artificial shoots by cuttings, and may obtain them from a single leaf as in the *Begonia*. A bit of root, as that of the dandelion, may also be stimulated to produce adventitious shoots.

General Descriptive Terms. A number of terms are used so that the stem may be described in an accurate and concise manner, and the following are some of the commoner ones. When the supporting tissue in the stem is strongly developed, the stem is said to be woody, otherwise it is herbaceous. The stem may be cylindrical, or it may be angular, and in the latter case it may be further distinguished as triangular, quadrangular, etc. It may be without hairs, and is then said to be *glabrous*, and if it has a peculiar bluish-green colour it is described as *glaucous* (e.g. fennel). When a hairy stem possesses hairs with swollen tops it is glandular (e.g. cranesbill); when the emergences are stronger than hairs the stem is bristly, or prickly if the emergences are very strong (Fig. 3). Spiny does not mean exactly the same thing as prickly, since *prickles* are only emergences from the skin of the stem, whereas *spines* are modifications of branches or leaves (Figs. 19 and 52), and cannot be pulled off so readily, in fact they have to be broken off. The portions where the leaves come off the stem are called *nodes* (Fig. 20), and if they are thicker than the intervening parts (*internodes*) the

stem is a knotted one. The stems (*culms*) of pinks and those of grasses are knotted, but in the latter the thickening appears to be some distance below the insertion of the leaf (Fig. 45). This appearance is deceptive, owing to the bottom portion

Fig. 20.—Stem-tendrils of Vine.

The stem is a sympodium, and the tendrils are modifications of the main axes, as indicated by the numbers. The place where the leaves come off is termed a node, the distance between two consecutive sets of leaves is termed an internode. *i*, internode; *n*, node. The numbers refer to the axes, thus the axis 1 terminates in the tendril 1 and so on.

of the leaf forming a kind of tube, which runs down the stem as a sheath for some distance. The stem of a grass, with the leaf sheaths rolled round it, is called a *haulm*.

Buds have been considered in Chapter II but their termin-

ology may be summarized here. The end bud terminating the main stem or a branch is a terminal bud; the buds on the side are lateral, or, since they are in the axils of leaves,

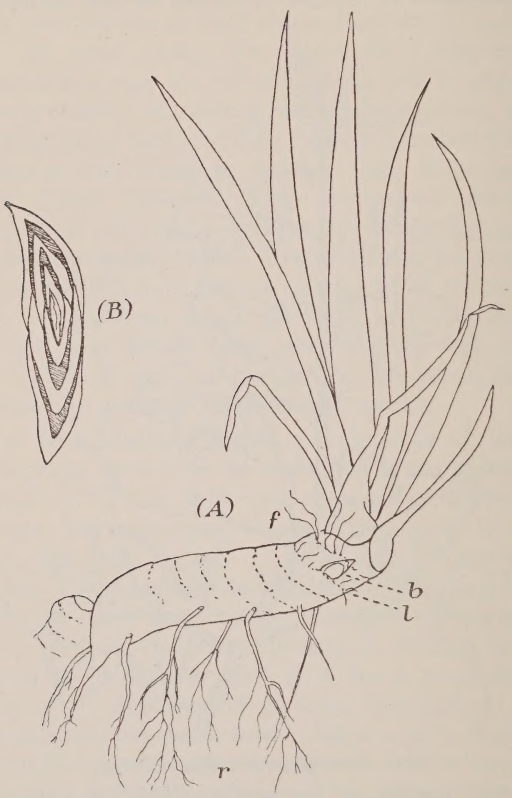

FIG. 21.

A, Rhizome of Iris. *B*, tranverse section of base of shoot, to show how the leaves are arranged. *b*, lateral bud in the axil of the leaf-scar *l*, which distinctly shows vein-scars; *f*, filaments from the veins, the other part of the leaf having decayed; *r*, adventitious roots.

axillary. Those developed in the ordinary method of acropetal are normal, those otherwise developed are adventitious. One may also speak of summer buds and winter buds, accord-

ing to the time of occurrence. Sometimes a bud which has been initiated normally has its growth arrested, owing to other buds being more favourably situated in regard to light, food or other influences. If these dormant buds later on proceed to grow they give rise to shoots, which appear to be adventitious, but are merely *deferred shoots.* The hedge-cutter assists in producing these deferred shoots as he cuts off the buds which were causing the food to be carried past the dormant buds. When an axillary bud becomes modified to form a tendril, or other body, an extra or *accessory bud* may be formed.

Modifications of the Stem

(1) **Underground Stems.** Many plants which perennate, or live on from year to year, have some part of the stem underneath the ground, serving as a storehouse for food. These underground stems can be distinguished from roots by their possession of leaves, which, however, do not develop as foliage leaves, unless they become exposed above the ground, but remain as scales. If the underground stem has a fairly even thickness (Fig. 21) it is called a **rhizome** (e.g. Solomon's-seal, iris, primrose, wood-sorrel). The thinner underground shoots of the couch-grass, sand-sedge (Fig. 22), lily-of-the-valley, etc., may be called slender rhizomes, and may sometimes extend far from the parent plant, thus acting not only as storehouses of food but also as a means of forming new plants. The subterranean growth of the sand-sedge may be traced for a score or more yards by the line of tufts which appear above the sand. A rhizome may be formed by the main stem growing more or less horizontally in the ground, its lateral buds, or some of them, forming erect branches, and it is then said to be a *monopodial* rhizome (e.g., wood-sorrel), but in many cases (Solomon's-seal, wood-anemone) the main stem grows horizontally for some time and then the terminal bud turns up to form a daughter plant, whilst a lateral bud develops to form the horizontal axis. This, in its turn, elongates upwards to form an apparently new plant, whilst a lateral bud continues the horizontal growth. The

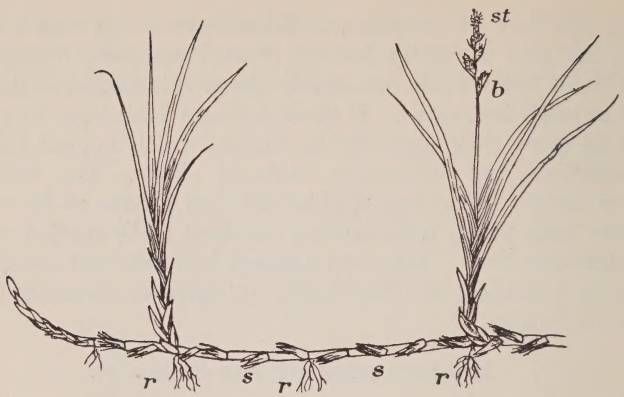

FIG. 22.—Slender Rhizome of Sand-sedge (*Carex arenaria*).

b, bract containing a pistillate inflorescence; *r*, adventitious roots; *s*, scale-leaves; *st*, staminate flowers.

rhizome is thus formed from a number of different axes, and is said to be a *sympodial* one. When the underground stem becomes swollen out in places **tubers** are formed, as in the potato and artichoke (Fig. 23).[1] When the underground shoot has the appearance of a large bud, it is said to be a **bulb** if the leaves are thick and fleshy, a **corm** (Fig. 26) if the leaves are thin and the axis (stem) thick. The onion is a *tunicated* bulb (Fig. 24) with juicy leaves wrapping like tunics round the thin stem; the lily is an *imbricated* bulb (Fig. 25) with the juicy leaves arranged like the tiles of a roof, whilst the crocus is a good example of a corm (Fig. 26).

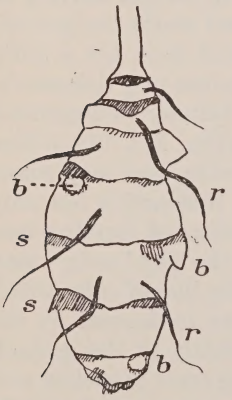

FIG. 23.—Stem-tuber of Jerusalem Artichoke.

b, buds in the axils of scale-leaves (note that the organic apex of the stem-tuber is directed downwards). *r* adventitious roots; *s*, scale-leaves.

[1] In this, and other places, where the artichoke is mentioned, the Jerusalem artichoke (*Helianthus tuberosus*) is the one referred to.

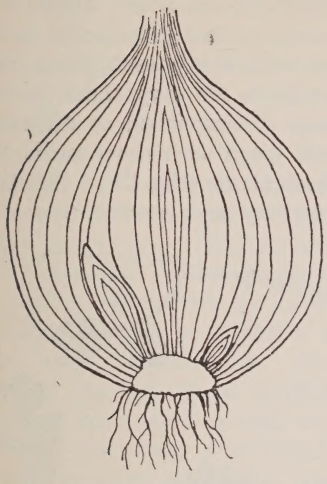

FIG. 24.—L.S. of Tunicated Bulb of Onion, showing adventitious roots and two buds.

FIG. 25.—Imbricated Bulb of Lily.

(2) **Runners and Similar Methods of Vegetative Reproduction.** In the creeping cinquefoil, creeping butter-

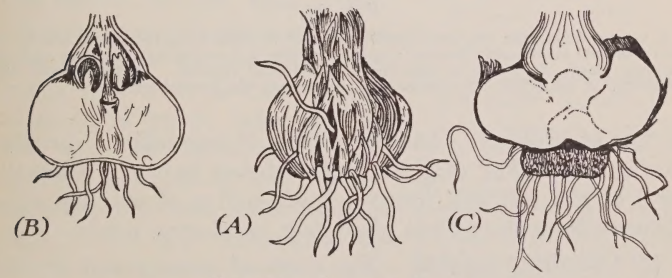

FIG. 26.—Corm of Crocus.

B and *C*, in longitudinal section; in *B*, two young corms for the following year are shown developing; in *C*, the old corm of the previous year is shown.

cup, strawberry, bugle and many other plants, the stem does not creep below the level of the soil, as it does in the sand-

sedge, but forms runners (Fig. 27) on the surface. Here and there some of the nodes form roots (which must, therefore, be adventitious), thus forming new centres of activity, and if the portions connecting them with the parent plant die away, new plants. When the runners are very short, as in the houseleek, they are sometimes distinguished as **offsets**. In the bramble the higher shoots often arch downwards to the ground, take root, and form fresh plants (Fig. 27). Similar shoots are produced by the gooseberry and currant, and are

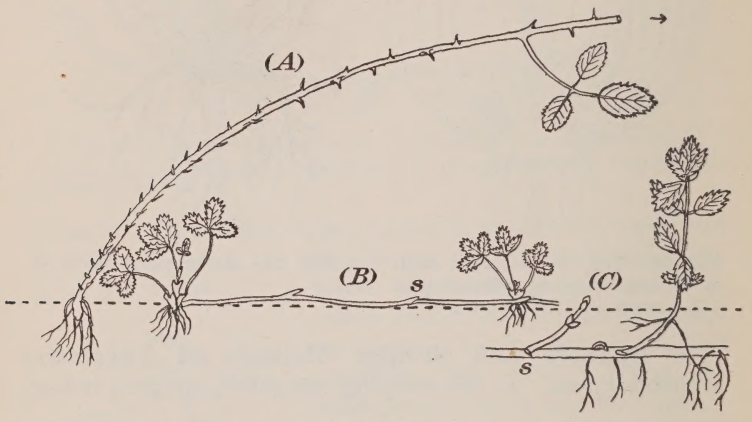

FIG. 27.

A, stolon of bramble, the arrow indicates where it comes from the parent plant. *B*, runner of wild strawberry, showing scale-leaves, stipulate and trifoliate leaves, and one daughter plant. *C*, sucker of mint from underground rhizome. Leaves opposite and decussate. *s*, scale-leaf. The dotted line represents the ground-level.

known as **stolons**. Another means of vegetative reproduction is the **sucker** (Fig. 27, *C*), which has its origin below the level of the soil and forms a fresh centre of activity some distance from the parent plant (e.g. raspberry, rose).

(3) **Climbing agents.** The stems of many plants are too weak to support the leaves and flowers borne on them, and, consequently, are in great danger of being smothered by their more robust or prolific neighbours. Some of these plants have acquired the power of using their neighbours for support. The bindweed, kidney-bean, hop, honeysuckle and

some other plants have **twining stems** (Fig. 28), which wind round the stems of neighbouring plants, and so reach towards the air and light. In the bindweed and kidney-bean the stem twines up the support in an opposite direction to that taken by the hands of a clock (counter-clockwise), but the stems of the hop and honeysuckle climb in a clockwise manner. In many plants the climbing is effected by means of slender threads or **tendrils** which are very sensitive to contact. When one of these tendrils is rubbed by a lead pencil, the side which has been stimulated becomes concave, and if the pencil is fixed so that the contact-stimulus continues, the tendril twists round it. The tendrils of the white bryony are often very conveniently situated in the hedges for observations of this kind. Tendrils may be modifications of either roots, stems or leaves. We have already met with tendrils which are modified roots, later on we shall consider those which are modified from leaves, but we are now concerned with stem tendrils (Figs. 20 and 29). These may be altered main shoots, or they may be developed from the lateral buds. In the vine (Fig. 20) the tendril is opposite to a leaf, and we might be inclined to consider it to be a modified leaf, but, if we examine a portion which does not bear tendrils,

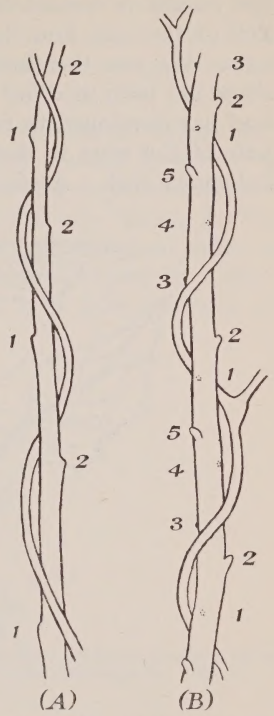

FIG. 28. — Twining-Stems (December condition).

A, hop twining in a clockwise manner round hazel stem in which the leaves had $\frac{1}{4}$ divergence. At the places shown by the numbers 1 and 2, buds are borne in the axils of leaf-scars. *B*, kidney-bean twining counter-clockwise round a stem of apple in which the leaves were arranged in $\frac{2}{5}$ divergence (see p. 62). Numbers 1, 2, 3, 4, 5, show where buds have developed in the axils of leaves: the position of buds at the back of the stem is indicated by dotted circles.

we find that the leaves are not opposite to each other. If the tendril is formed from a branch it ought to be in the axil of the leaf, and that position is occupied by the main axis. We are therefore forced to consider that the main shoot has been modified to form a tendril, whilst the axillary bud has developed to function as the main axis. The main axis of the vine is then a sympodium like the rhizome of Solomon's-seal. A similar method of tendril-formation is

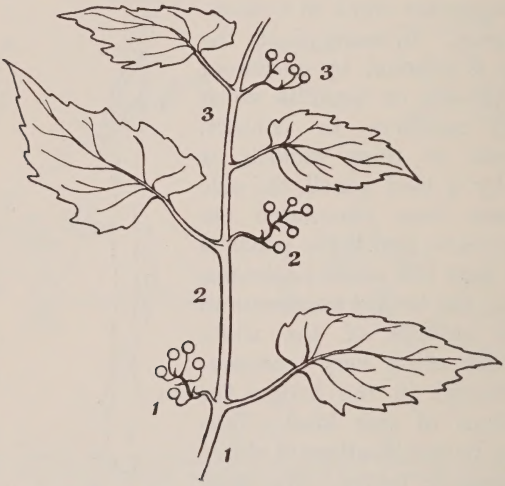

FIG. 29.—*Ampelopsis.*

The stem is sympodial (cf. Fig. 20), the modified main axes bear sucker-discs. Note that the position of one of the small leaves on the tendril is opposite to the "branch" which is forming a sucker-disc.

adopted in the *Ampelopsis* (often known as the Virginian creeper), the terminal bud developing into a branched tendril whilst a lateral bud continues the main axis of the plant. In the *Ampelopsis* the tips of the tendrils have been further modified to serve as **adhesive suckers** (Fig. 29). In the passionflower and white bryony the tendrils are in the axils of leaves, and therefore have been developed from lateral buds and are modified branches.

(4) **Spines or Thorns.** These protect the plant from browsing animals. In the hawthorn and sloe the spines (Fig. 19) must be modified stems, as they are borne in the axils of leaves, and may sometimes be found bearing leaves or buds.

(5) **Cladodes.** When, for some reason or other, the leaves have been reduced, so that they cannot do the work which is usually done by leaves, the stem may become leaf-like. Such leaf-like stems or cladodes are shown in the butcher's broom (Fig. 30), and their morphological value is evidenced from the following characters shown in them: they do not set themselves so that light falls on them at

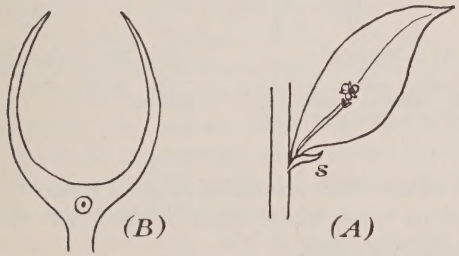

FIG. 30.

A, cladode of butcher's broom, borne in the axil of the scale-leaf (*s*) and bearing modified leaves and a pistillate flower. *B*, stipule-spine of *Acacia sphærocephala*. The base is hollow, and used by ants as a habitation.

right angles to their surfaces, they are borne in the axils of scale-leaves and they bear small scale-leaves and flowers.

(6) **Bulbils.** Some plants bear little bud-like bodies in the axils of their leaves. When these little bulbs or bulbils fall off they grow into new plants, if conditions are favourable. The lesser celandine often flowers and fruits under conditions which are unfavourable for the proper ripening of its seeds, and its propagation by means of seed is rather precarious. Its seed method of reproduction is supplemented, as we have seen, by tuberous roots, but, besides these little swellings below the ground, similar smaller bodies (bulbils) are formed in the leaf-axils. In the crow garlic, the stem, instead of

bearing a bundle of flowers at the top like most garlics do, often bears a crowded head of little bulbs or bulbils. The bulbils of the lily (Fig. 31) are formed from ordinary vegetative

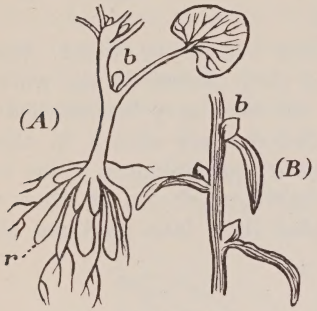

FIG. 31.—Bulbils.

A, lesser celandine with bulbils (*b*) similar to the tuberous roots. *B*, *Lilium* with bulbils (*b*) taking the place of buds.

FIG. 32.—Crow-garlic bulbils.

The bulbils take the place of flowers.

buds, those of the lesser celandine (Fig. 31) must be considered as adventitious roots, whilst those of the garlic (Fig. 32) take the place of flower-buds.

CHAPTER VI

THE LEAF AND ITS FUNCTIONS

During our examination of the seed and seedling, minute leaves were noticed on the plumule, whilst one or more seed-leaves, or cotyledons, were modified to serve as storehouses of food. As the plumule gets larger the minute leaves expand and become ordinary foliage leaves, but the cotyledons gradually shrink as their store of food is used up, and finally wither away. This is eventually true of the cotyledons in any case, whether they remain below the surface of the soil or rise up on their hypocotyls and become green. In the latter case they certainly function as true leaves for a time, but their ultimate fate is the same.

In addition to the leaves, which were already present on the plumule, other primordia (or beginnings) are initiated, so that there is a further addition to the number of leaves, according to the nature and size of the plant. When the addition to the number of leaves is a continuous one, the shoot is always terminated by a bud. Each primordium develops at first into a little bump on the outside of the stem, and this may be considered as a **leaf-base**; then the leaf-blade or **lamina** develops, and finally an intermediate leaf-stalk or **petiole** may be produced. This order of development is often of great service to the plant when an expanded leaf-base becomes precociously mature, and more or less encloses the delicate and folded-up lamina. In the cow-parsnip, or hogweed, the expanded leaf-base (Fig. 33) not only protects the infant leaf-blade, but often the young flower-buds as well. In some cases the leaf-base expands into definitely shaped leaf-like organs, which are known as **stipules** (Fig.

39, *F*), and as these mature early they form a kind of protective hood to the parts which appear later. An extreme

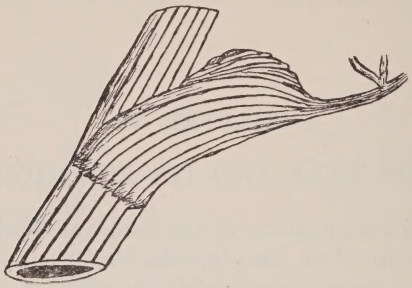

FIG. 33.—Protective Leaf-Base of Hogweed (*Heracleum sphondylium*).
The leaf is not drawn, only t hree leaflet stalks being shown.

example of a protective chamber formed by the stipules is shown in the tulip-tree (Fig. 34), where the stipules of one

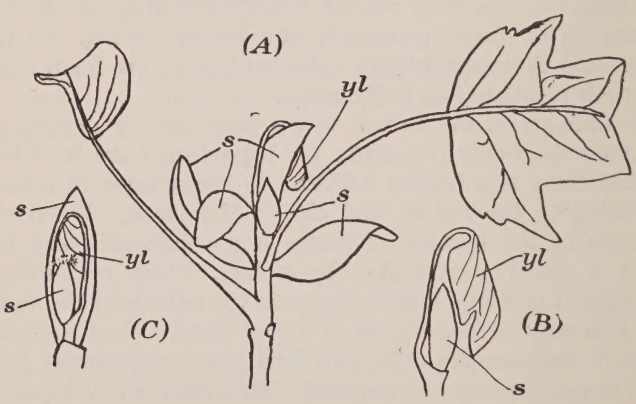

FIG. 34.—Tulip-tree, showing Stipules enclosing young leaf.

A, shoot showing two pairs of stipules which have opened out and the stipules enclosing the bud. *B*, top portion of *A*, with all stipules, except tl ose enclosing the bud, removed. *C*, enlarged view of (*s*) in *B*, opened out so as to show the folded young leaf and stipules protecting the bud. *yl*, young leaf; *s*, stipule.

leaf not only completely enclose the remaining portions of that leaf, but also the chambers formed by the stipules of younger leaves.

Experiment 21. To show that leaves give off water. Obtain six fresh ivy leaves, put their stalks through a hole in a piece of cardboard and pack with cotton-wool. Place the cardboard and leaves on the top of a vessel so that the petioles are in the water. Cover with a bell-jar. Use a control apparatus without the leaves and leave for a few hours. Observe that the moisture on the inner face of the bell-jar with the leaves is greater than in the control. The process is known as transpiration.

Experiment 22. To show that transpiration is chiefly effected by the under surfaces of many leaves. Dry a strip of cobalt paper (which is pink when damp and blue when dry), and double it over an ivy leaf, so that half is on the upper and half is on the lower surface. Cover with a larger strip of dry mica, similarly doubled over, and fasten with wire clips so as to exclude the air. Notice that the cobalt paper on the under side of the leaf becomes pink much more quickly than that on the upper side. If the ivy is growing outside, a suitable day must be chosen for this experiment, and care must be taken to prevent the humidity of the air from acting on the cobalt paper, as moist air quickly turns it pink.

Experiment 23. To determine the rate of transpiration. Fit up an apparatus (potometer) as figured (Fig. 35, 1), completely fill with water, stop the lower end with the finger and push the cork containing the plant *P* into the top end, taking care that no air gets in. Place the lower end of the capillary tube *C* in the water of the dish *D* and leave for a few minutes. Lift the capillary tube out of the water, allow a bubble about 8 mm. long to form and then replace the tube. Observe the rate of progress of the bubble by means of the graduated scale *B*, first noting that the rate is a steady one. Obtain the volume or the weight of water in one centimetre of the capillary tube by measurement or weighing, and calculate the rate of transpiration. A branch of lime is suitable for this experiment if it is available. During winter time a branch of the cherry laurel gives fairly good results. In any case the branch must be cut off under water, as the air in the tissues of the plant may be at a pressure less than that of the atmosphere. If the branch were cut off in the air, more air would enter, and the normal transpiration of the plant might be interfered with.

Experiment 24. To show how external influences affect the rate of transpiration. In a similar way to that adopted in Expt. 23 fit up the potometer figured (Fig. 35, 2) (or the potometer used previously may be employed) though the

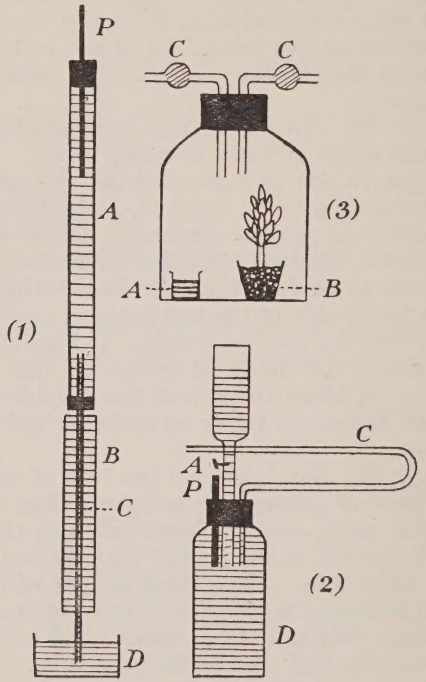

Fig. 35.

1. Potometer. *A*, tube filled with water and containing a branch, the stem of which is indicated at *P*; *B*, graduated scale; *C*, capillary-tube; *D*, dish containing water. 2. Horizontal potometer: references as above. *A* has a stop-cock, by which the head of water is able to force the air back along the capillary-tube. 3. Apparatus for showing that carbon dioxide is necessary for the formation of starch. *A*, vessel containing potassium hydrate; *B*, pot containing a plant in soil; *C*, bulbs containing solid caustic potash.

capillary tube is not placed in a dish of water. Note the number of seconds necessary for the air to travel a distance of 5 cm. along the capillary tube when the plant is exposed to different external conditions. Note that an increase of temperature or brightness quickens the rate of transpiration.

The tube *A* has a stop-cock, by which the head of water can be allowed to force the air back along the capillary tube, so that many experiments can be performed with the same plant.

EXPERIMENT 25. To show that plants take in oxygen and give out carbon dioxide. Get two jars and put some peas in a little water at the bottom of each jar, cork, and allow the peas to germinate for twenty-four hours. Test the gas in one of the jars with a lighted splint. Pour the gas from the other jar into a test-tube containing a little limewater, and shake up. Two other jars with water only in them may be used as controls if necessary. The process of taking in oxygen and giving out carbon dioxide is known as breathing or respiration.

EXPERIMENT 26. To show that respiration goes on in the dark. Repeat Expt. 25, except that the jars are kept in the dark. Another method is by means of the apparatus figured (Fig. 36). *A* is a rubber-stoppered flask containing some peas, a small tube holding potassium hydroxide (*K*), and a little water; *B* is a vessel containing a coloured liquid. The potassium hydroxide absorbs the carbon dioxide produced, and the coloured liquid is drawn along the tube. The flask end of this tube may be hooked, so that the caustic potash tube can be fastened to it.

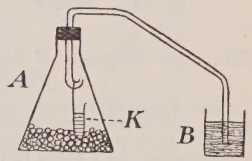

FIG. 36. — Diagram of Apparatus for showing Respiration.

(For references see Expt. 26.)

EXPERIMENT 27. To show the respiration of leaves and other green organs. Place some leaves with a little water in a large flask, and lower a test-tube containing a little lime-water into the flask. Tightly close the flask with a rubber stopper, and keep in the dark for twelve hours. Note the turbidity which is produced when the lime-water is shaken up. The necessity for keeping the green structures in the dark will be realized after Expts. 33–4 have been done. (Also see p. 55.)

EXPERIMENT 28. To estimate the amount of oxygen used by a plant during respiration. Fit up the apparatus shown (Fig. 37), using rubber stoppers and connections. Place some green leaves in the large glass jar, and then pass a current of air through the apparatus fitted up in series except *d* and *e*.

Join the vessels *d* and *e* in the series, cover the large jar with a cloth, and aspirate air through for an hour. Titrate the original baryta water and also the liquid in *d* with a standard solution of oxalic acid, using a few drops of phenolphthaleine solution as indicator. This apparatus has an historical interest, as it is similar to that used by Sachs, who was a pioneer in the study of vegetable physiology.

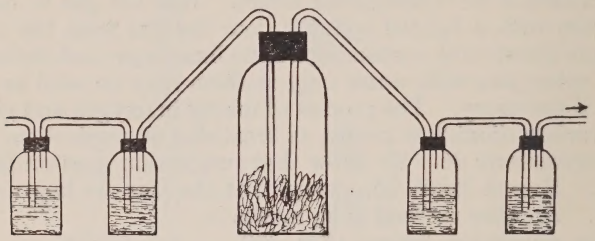

FIG. 37.—Diagram of Apparatus to estimate the Amount of Oxygen given off during Respiration.

a and *e*, contain caustic potash solution; *b* and *d*, baryta water; *c*, leaves and a little water. The arrow indicates where the apparatus is joined on to an aspirator. *a*, potassium hydroxide solution for absorbing the carbon dioxide of the air; *e*, potassium hydrate solution acting as a guard in case a backward flow of air occurs.

EXPERIMENT 29. To show that the respiratory ratio $\left(\frac{\text{amount of carb. diox. evolved}}{\text{amount of oxygen used}}\right)$ in normal respiration equals one. Fit up two similar tubes ($\frac{3}{4}$–1 inch diam.) as shown (Fig. 38). In one, place some pellets of wet blotting-paper and some germinating peas. Treat the other similarly, except that the peas are killed by boiling in a dilute solution of salicylic acid which also ensures the death of any germs present.

Leave for some time, and notice if any change takes place in the level of the coloured liquid in the small delivery tubing. Any change in the control must be due to atmospheric changes. If the other tube has a similar change, the respiratory change = 1. Carbon dioxide is slightly more soluble in water than oxygen is, but this will scarcely affect the result.

EXPERIMENT 30. To show that heat is produced during periods of active respiration. In the centre of a wide glass trough, with a shallow layer of dilute potassium hydroxide solution at the bottom, place a narrow beaker half-full of

germinating barley. Cover with a bell jar, so that the bulb of a thermometer, fitted through the cork of bell jar, is just above the level of the barley in the beaker. Fit up a control in which the barley has been killed by boiling in a dilute solution of salicylic acid.[1] Observe that the temperature becomes higher in the apparatus containing the germinating barley. Field observations on the temperature inside the spathe (Fig. 87) of a cuckoo-pint during the growth of the flowers may also be made. The temperature may be 2° C. higher than that of the surrounding air.

Experiment 31. To show that starch is present in leaves which have been exposed to sunlight for some time. Soften the leaves by boiling them for one minute, and then extract the green colouring matter (chlorophyll) from them by warming in alcohol for five or ten minutes. Wash the decolorized leaves, and put them in a white dish with iodine solution. As other substances besides starch are present in the leaf, the colour produced cannot be expected to be such a good blue as in an ordinary starch test. Clover leaves usually give good results.

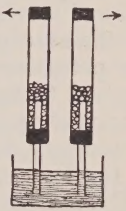

Fig. 38.—Diagram of Apparatus to show the Respiratory Ratio (see Expt. 29).

The arrows indicate where the tubes are clamped.

Experiment 32. To show that the starch disappears from the leaf during the night. Repeat the previous experiment on one leaf of the plant, then take a leaf from the plant at the dawn of the following day, or place the plant in a dark cupboard for about twelve hours and take another leaf from it. Test for starch. Instead of using whole leaves each time, half of the leaf may be tested in the afternoon and the other half next morning.

Experiment 33. To show that light is necessary for the formation of starch in leaves. Place a piece of tinfoil with some pattern cut in it over a leaf of a geranium plant, cover with mica and clamp. Expose for several hours to sunlight, and then test the leaf for starch. Note the " starch printing " in the exposed parts of the leaf.

[1] This experiment may be performed by putting the barley seeds into two thermos flasks.

Experiment 34. To show that chlorophyll is necessary for the formation of starch in leaves. Obtain some variegated leaves of *Pelargonium* which have been in sunlight for some time and test for starch. Note the absence of the blue reaction in the parts of the leaf which were colourless. The variegated leaves of periwinkle or ivy may be used, but they take a long time to decolorize.

Experiment 35. To show that carbon dioxide is necessary for the formation of starch (photosynthesis). Fit up the apparatus shown (Fig. 35, 3). Keep the plant in the dark, and show that no starch is present in one of the leaves. Before placing the plant and its pot in the apparatus, put them under the air pump, so as to remove any carbon dioxide from the soil and leaves, and keep in the dark. After a sufficient time for the absorption of any carbon dioxide in the apparatus by the potassium hydrate has been allowed, the apparatus is exposed to light for some time, and a leaf tested for starch. A control apparatus without the potash vessels may be used, if necessary, to show that, when carbon dioxide has free access to the leaves, starch is formed.

Experiment 36. To show that oxygen is evolved during photosynthesis. Place some water-plants (*Elodea* or other pondweed is suitable) under a funnel with a short stem. Immerse the funnel in a glass trough of water, and place a test-tube, filled with water, over the stem of the funnel. Leave in bright sunlight for a few hours, and test the gas, which has appeared in the test-tube, with a glowing splint. If the experiment is prolonged to another day, it is advisable to add some Sachs' solution to the water, and pass some purified carbon dioxide through it.

Functions of the Leaf. The leaves are the main agents by which three of the chief processes of plant-life are performed. They are the organs of breathing, or respiration, obtaining oxygen from the air and giving off waste carbon dioxide ; they are the agents by which transpiration is effected, superfluous water being got rid of, and they are the means whereby carbon-assimilation or photosynthesis is accomplished. The stem may assist in any of these processes, and the root cannot work well unless it is able to breathe, but the leaves are specially fitted for these kinds of work. They have a large surface area, by which gases can be taken in or given off,

and, as we shall see later on (Chap. XVII), the internal structure enables gases to pass freely in the interior of the leaf.

Respiration. Breathing, or respiration, is essential to normal life, either in animals or plants. The energy by which a locomotive is driven along is derived from the burning of coal, gas, oil or other material, the carbon and hydrogen present in the combustible substance being oxidized and energy liberated. The oxidation of carbon and hydrogen may be expressed by the equations $C + O_2 = CO_2$ and $2H_2 + O_2 = 2H_2O$, but these equations do not represent the whole story. If we take into account the physical results, the equations should read $C + O_2 = \text{Energy} + CO_2$ and $2H_2 + O_2 = \text{Energy} + 2H_2O$, the carbon dioxide and water being merely the waste products of a process whereby energy is produced. Animals and plants, whenever they do any kind of work, must obtain energy, and this is usually obtained by the oxidation of carbon and hydrogen from the tissues of the body. Breathing, or respiration, is merely a method whereby oxygen can be supplied to the tissues in the working part of the body, and the waste carbon dioxide taken away.

Nutrition, or Feeding. The substances which are used up in the cells of the plant must be replaced if the plant is to continue its activities. The nitrogenous and mineral substances required are taken up by the roots, whilst the carbonaceous material is supplied by means of the leaves. This assimilation of carbon can only occur in green plants (Expt. 34), and in the presence of light (Expt. 33). It is not an easy matter to make experiments showing the different stages of the process, but as the end-product is often starch, the conditions necessary for the process can be studied by making use of the blue reaction which starch gives with a solution of iodine in potassium iodide. The air contains a small amount of carbon dioxide, and, in some way or other, the leaf is able to cause water and this gas to interact, so that starch is produced. The equation representing this complete process may be given by $6CO_2 + 5H_2O = C_6H_{10}O_5 + 6O_2$, since $C_6H_{10}O_5$ is the empirical formula of starch, but, in order for the carbon dioxide and water to interact together, energy

must be supplied, and as this energy must come from a source outside the plant, we ought to write the equation $6CO_2 + 5H_2O + \text{Energy} = C_6H_{10}O_5 + 6O_2$. As plants are unable to manufacture starch without light, it seems probable that light supplies the energy required. The green colouring matter (**chlorophyll**) is also essential, since it serves as a medium for the absorption of light. Owing to the necessity of light for the assimilation of carbon, the process is often called photosynthesis, which literally means light-building.

Chemical Changes during Photosynthesis. It is probable that the first chemical change which takes place is the formation of formaldehyde,

$$CO_2 + H_2O = \underset{\text{Formaldehyde.}}{H.CHO} + O_2,$$

but the formaldehyde is a poison to the plant, and is quickly combined together (polymerized) to form sugar. When the sugar formed is grape sugar, the change may be represented by

$$6\ H.CHO = C_6H_{12}O_6.$$

Sometimes the process gets no further, and the amount of carbon assimilation is a limited one; when the sap of the leaf contains as much sugar as possible, photosynthesis must stop. Usually the soluble sugar is changed into insoluble starch,

$$C_6H_{12}O_6 - H_2O = C_6H_{10}O_5,$$

the concentration of the sugar in the sap is reduced, and further sugar can be manufactured.

Translocation of Food. During the night, when photosynthesis cannot go on, the cells of the leaf are still working, but in a different manner. The food, which has been made during the day, is conveyed to the parts of the plant which require it (Expt. 32), though this, of course, also went on in the daytime, when the production of carbonaceous food was far in excess of the transport service. The insoluble starch cannot be carried away as starch, since the transport service can only deal with substances which are soluble in water, therefore the first work to be done is to change the insoluble starch into something which is soluble in water. In the leaf

there is a ferment (**diastase**), which is capable of changing the starch into sugar, and the unloading of the leaf goes on during the night (Expt. 32). It should be noted that the waste product of breathing is carbon dioxide, which is the substance required for feeding purposes, whilst, on the other hand, the waste product of photosynthesis is oxygen which is the material required for breathing. During the night, when no photosynthesis is occurring, carbon dioxide is given out by the plant, but when the light is strong enough, the gas evolved is oxygen, hence the necessity for keeping the apparatus in the dark during our respiration experiments with bodies containing chlorophyll (Expts. 27–8). It is possible that the conditions may be such that no gas whatever is given off, the two processes balancing each other.

Transpiration. The third main function of the leaf is to give off water vapour. That a large amount of water must be given off by the leaves of a plant, in order to obtain sufficient food, is evident when we consider that all the food substances absorbed by the root-hairs are in very dilute solution. Transpiration is then an excretory process, the water being given off whilst the salts are retained. Most leaves are **dorsiventral,** i.e. they have an upper surface distinctly different from the under parts, and the water vapour is chiefly given off from the undersides where the conditions are more regular (Expt. 22). In plants where the leaves are erect, or nearly so, the minute openings (**stomata**) are more evenly distributed (see Chap. XVII). On a hot day more water is given off than on a cold day, and other external influences, such as wind, light and humidity of the air, can be shown by experiment (Expt. 24) to affect the rate of transpiration. It is not quite correct to consider transpiration as an excretory method only. A large supply of water is essential to the plant in other ways than for food transport. The rigidity of a plant depends on the cells being swollen with water, and growth cannot occur except under such conditions. The vaporization of the water in the plant may also keep the temperature more constant.

CHAPTER VII

THE LEAF, ITS CHARACTERS AND MODIFICATIONS

The characters of a leaf cannot be exactly compared with those of roots and stems, but, as far as possible, their distinguishing characters will be given in the same order as for the root and stem.

Distinguishing Characters

(1) A leaf usually bears a bud in its axil. It does not bear any buds, either vegetative or floral, on its surface.

(2) A leaf usually takes a form different from that of its axis, and in its young state is usually protected by being folded up.

(3) The orientation of the leaf is little affected by geotropism or hydrotropism. The surface of the leaf usually makes a right angle with the incident rays of light. This is generally true of dorsiventral leaves, but the leaves of monocotyledons are often more or less erect.

(4) The leaf has an exogenous origin, and usually grows faster in its young state than the stem from which it came.

(5) The internal microscopic structure is characteristic (Chap. XVII).

(6) Leaves are produced in acropetal succession.

General Descriptive Terms. In order to describe a leaf in an accurate and concise manner a number of terms relating to shape, margin, veining and other characters are employed. Those which are most general and useful are given below. In regard to shape the leaf may be *linear*, e.g. grass (Fig. 45), lance-shaped or *lanceolate*, e.g. ribwort,

plantain (Fig. 39), egg-shaped or *ovate* (Fig. 1, *B*) with the broad end towards the stalk, e.g. thyme, heart-shaped or *cordate*, e.g. nettle (Fig. 39), kidney-shaped or *renate*, e.g. lesser celandine (Fig. 31), circular or *orbicular* (Fig. 41, *A*), e.g. pennywort, arrow-shaped or *sagittate*, e.g. sorrel (Fig. 39,

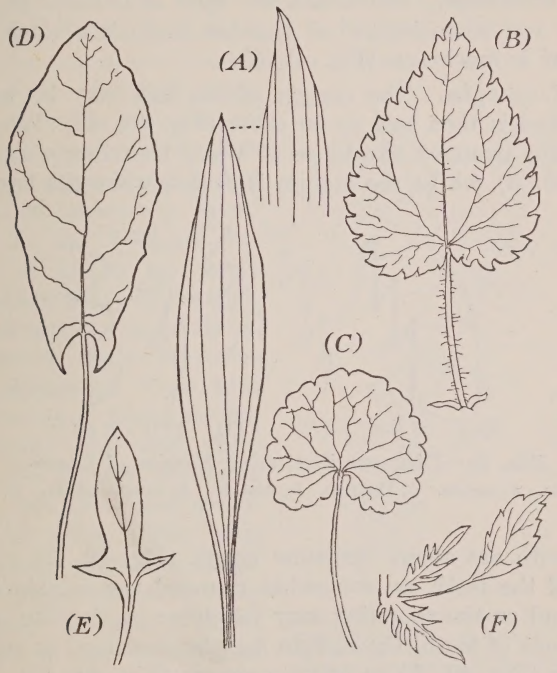

FIG. 39.—Leaf Shapes.

A, lanceolate leaf of ribwort-plantain with entire margin, parallel venation and acute apex. *B*, cordate and stipulate leaf of nettle with crenate margin and reticulate venation. *C*, renate leaf of ground-ivy with crenate margin and palmate venation. *D*, sagittate leaf of sorrel with pinnate venation. *E*, hastate leaf of sheep-sorrel. *F*, ovate and stipulate leaf of pansy.

D). A *hastate* leaf is somewhat similar to a sagittate one, but the cusps or points at the base of the leaf, instead of running down more or less parallel to the petiole, are at right angles to it, e.g. sheep's-sorrel (Fig. 39, *E*). An egg-shaped leaf with the narrow end near to the petiole is said

to be *obovate*, and other terms such as *acicular* or needle-shaped, elliptic, oblong, triangular, etc., are also used. The apex of the leaf may be blunt or *obtuse* (Fig. 39, *C*), or it may be *acute* (Fig. 39, *A*). When the apex tapers very gradually to a sharp point, as in the leaf of a grass (Fig. 45), it is said to be *acuminate*. Sometimes the apex is notched or *emarginate*, and when instead of a notch there is a small tooth the leaf is *mucronate* (Fig. 41, *C*).

Leaf-margin. The margin of the leaf may be without teeth and is then said to be *entire* (Fig. 40, *A*). When the teeth are arranged like those of a saw the margin is *serrate* (Fig. 40, *B*), whilst the margin is *dentate* when the two sides

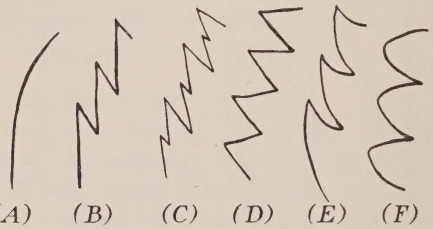

FIG. 40.—Diagrams illustrating Margins of Leaves.

A, entire. *B*, serrate. *C*, biserrate. *D*, dentate. *E*, crenate-serrate. *F*, crenate-dentate.

of a tooth are about the same length (Fig. 40, *D*). If the sides of the teeth are somewhat rounded the margin is *crenate*, and as the rounding may be either on dentate or serrate kinds of teeth, the margin may be described as crenate-dentate (Fig. 40, *F*) or crenate-serrate (Fig. 40, *E*).

Venation. The veins of the leaf in grasses, lilies and most monocotyledons are more or less parallel to each other, and therefore the veining or venation is said to be *parallel*. In most dicotyledons the veins branch and appear to form a network in the leaf, which is then said to be net-veined (Fig. 39, *B* and *C*) or to possess a *reticulate* venation. When the main vein passes up the centre of the leaf and gives off branches in the same way as in a feather the venation is *pinnate* (Fig. 39, *D*) ; when the main vein forms a number

of branches at the base the venation is *palmate*, e.g. ivy (Fig. 1), ground ivy (Fig. 39, *C*).

Divisions of the Leaf. The leaf may be *simple* or it may be divided up into a number of smaller portions which are called leaflets (Fig. 41, *B*), and then the leaf is said to be *compound*. The term compound is applied to the leaf when the divisions extend right to the petiole or its continuation, but when the divisions are shallower the leaf is simple and lobed. The lobing may occur in either a pinnate or a palmate manner, so that the leaf may be pinnately lobed or palmately lobed (Fig. 1, *A*). Different degrees of lobing are sometimes described as pinnatifid, pinnatipartite, pinnatisect, palmatifid, palmatipartite, or palmatisect, those with the shallower lobing having the suffix -fid, and those with the deepest the suffix -sect, but the exact meanings of these terms vary according to personal usage. In a compound leaf the leaflets may be again divided, and it is then said to be bipinnate; if further division occurs it may be tripinnate.

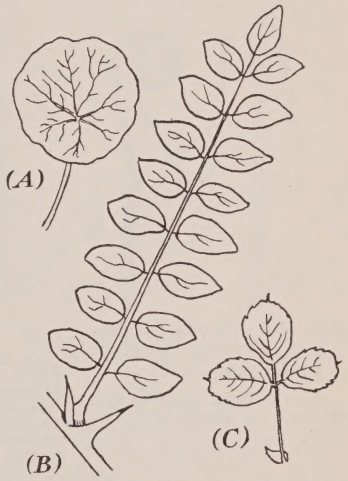

FIG. 41.

A, orbicular and peltate leaf of Indian-cress (*Tropeolum*). *B*, pinnate leaf of false acacia with stipule-spines. *C*, trifoliate and stipulate leaf of medick (*Medicago maculata*) with mucronate apices to the leaflets.

When the leaf has a stalk it is *petiolate*, but when the stalk is absent it is *sessile*. If a leaf-base has little outgrowths or stipules (e.g. nettle, Fig. 39, *B*) the leaf is *stipulate*; when these are wanting it is *exstipulate*. When the leaf is compound, the continuation of the axis beyond the insertion of the basal leaflets is known as the *rachis*.

Prefoliation. The leaves, when young, are often folded together so as to be protected from the effects of cold, wet

and other external conditions. When the leaf has emerged from the bud, this prefoliation, as it is called, causes less surface to be exposed to the air, and excessive transpiration is less likely to occur. *Circinate* prefoliation, when the apex

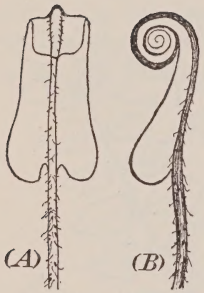

FIG. 42.—Hart's-tongue-fern, showing Circinate Prefoliation.

A, view from upper surface of frond. *B*, profile view.

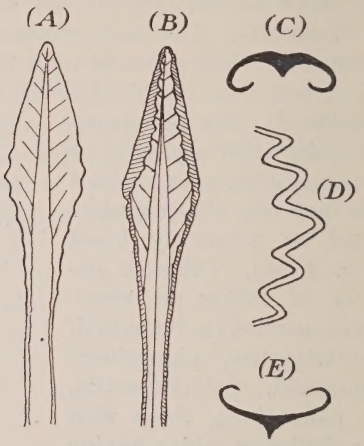

FIG. 43.—Prefoliation.

A, upper surface of primrose leaf. Note the length of the leaf base and that the leaf stalk has scarcely developed. *B*, under surface. The revolute margin is indicated somewhat diagrammatically by shading. *C*, section through leaf of primrose. *D*, section through plicate leaf of horse-chestnut. *E*, section through involute leaf (e.g. cuckoo-pint.)

of the leaf is rolled downwards, occurs in the ferns (Fig. 42); *plicate* or folded prefoliation is found in the horse-chestnut (Fig. 43, *D*); *revolute* prefoliation, when the sides of the leaf roll inwards towards the under surface, is shown by the dock and primrose (Fig. 43, *A*, *B*, *C*), whilst the young leaves of the cuckoo-pint exhibit *involute* prefoliation (Fig. 43, *E*), the sides rolling towards the upper surface of the leaf.

Leaf-arrangement or Phyllotaxis

In many plants (e.g. daisy) the stem is very short and the leaves appear to come from the root and therefore are said to be *radical*, but in most plants the stem is longer, and the leaves borne by it are *cauline* or stem-leaves. The leaves may be

arranged in groups of two or more at the same level on the stem (Fig. 44), when they are said to be *whorled* (*cyclic*), or there may be only one leaf at each node, and a line passing round the stem and through the bases of the leaves would describe a spiral, so this arrangement is appropriately known as *spiral* (*acyclic*). The most common kind of whorled arrangement is shown in the horse-chestnut (Fig. 4) and dead-nettle (Fig. 47) where two leaves are opposite each other at the

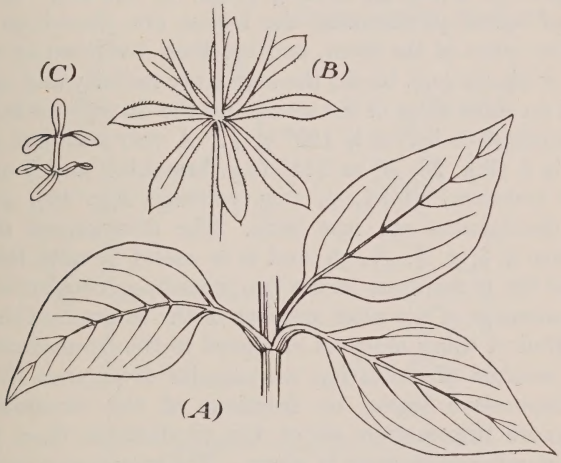

FIG. 44.—Whorled Leaves.

A, three-whorled leaves of Jerusalem artichoke. *B*, cleavers; eight leaves appear to be present in the whorl; those with shoots in the axil are true leaves, the others are usually regarded as stipules. *C*, portion of Elodea, showing alternating whorls of three leaves.

same node, and the next pair of leaves are at right angles to them, such an arrangement being an opposite and decussate (crossing) one. In some pondweeds the whorls are superposed, i.e. each pair of leaves are so placed that a straight line passes through the leaf-bases at consecutive nodes on the same side. In the juniper, elodea and artichoke (at least in part) there are three leaves in a whorl (Fig. 44), and, in the bedstraw, the whorl appears to have four or more leaves (Fig. 9), though some of these apparent leaves are better considered

as stipules. In an acyclic arrangement the leaves alternate with one another in different ways, and it is useful to take the angle between consecutive leaves as an index of arrangement.

Some Common Divergences. In some plants (e.g. hazel) the leaves are *distichous*, or equally arranged on two sides of the stem, with an angular divergence of 180°, or half the circumference between two consecutive leaves, and the divergence is briefly given as $\frac{1}{2}$ (Figs. 28 and 45). In other cases of spiral phyllotaxis, the leaves are placed on more than two sides of the stem, and are then described as *radial*. In a few plants (e.g. birch) the leaves are radially and equally spaced on three sides of the stem, and the divergence between two consecutive leaves is 120° or $\frac{1}{3}$. A very common divergence is $\frac{2}{5}$ (Fig. 28, *B*) or 144° (e.g. bramble), and $\frac{3}{8}$ or 135° is also common, whilst, $\frac{5}{13}$ (e.g. cabbage, Fig. 46), $\frac{8}{21}$, and other divergences are met with. The divergences of this series are $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, and it is useful to note that the sums of the numerators in the two preceding divergences form the numerator of the next member of the series, and that the same kind of thing happens in regard to the denominators.

The method of indicating the angular divergence between two consecutive leaves by fractions of the circumference gives more information about the phyllotaxis than if the actual number of degrees is given. The numerator indicates the number of times we must trace the spiral round the stem before we come to a leaf exactly above the one we started with, whilst the denominator shows the number of leaves passed through, and the number of rows of leaves on the stem. An old cabbage stem, in which the leaf-scars are used for tracing the spiral (a piece of string may be wound round so as to pass through the middle of each leaf-scar), forms an excellent exercise in the determination of phyllotaxis (Fig. 46). The wallflower, or an upright branch of the bramble, rose or ivy, usually show the phyllotaxis quite clearly, but it must be noted that upright shoots which have been fairly equally illuminated on all sides should be chosen, otherwise great care must be taken to ensure that the stem is straightened

out properly, and that the actual positions of the leaf-bases, and not the apparent positions of the leaves, are taken. The creeping shoots of ivy appear to have a divergence of $\frac{1}{2}$, but careful examination shows that they are arranged in a $\frac{2}{5}$ manner. In some plants, such as the yew, the shoots appear to be dorsiventral, the back being quite distinct from the front, but careful examination will show that the dorsiventrality is only apparent, as the leaves are not fixed in a distichous manner. The amount and direction of light has a great influence on the apparent divergence, as can be

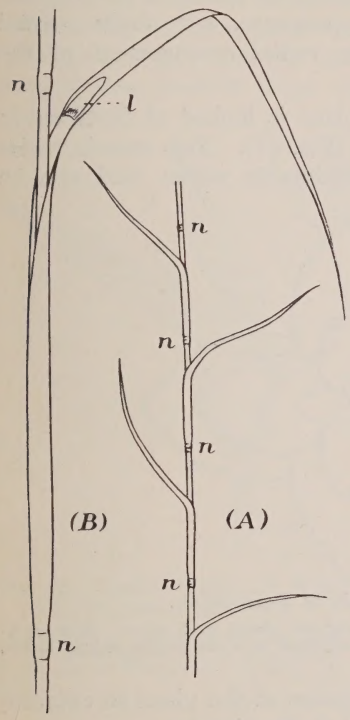

FIG. 45.

A, linear and distichous leaves of a grass (*Poa trivialis*) with sheathing leaf-bases (the internodes are somewhat shortened). *B*, a leaf pulled out so as to show the sheathing base split on one side and the large ligule (*l*). *n*, nodes.

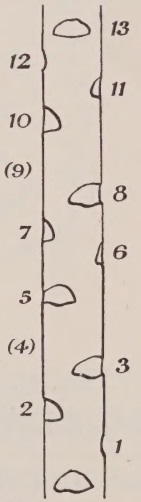

FIG. 46.—Cabbage-stump, showing $\frac{5}{13}$ Divergence.

The 4th and 9th leaves are at the back and therefore not shown. Buds had developed in a few axils, but are not included in the figure.

noted on examining the plants which have been previously mentioned, or by noting the different appearances presented by such plants as the whortleberry when growing under different conditions. In the shade, the shoots of the whortleberry have a dorsiventral appearance, but under normal conditions of illumination the radial arrangement of the leaves is manifest.

Leaf-mosaic. When the plant is looked at from above a mosaic of the leaves is seen (Fig. 47). This mosaic varies in different plants as the phyllotaxis varies, and can be

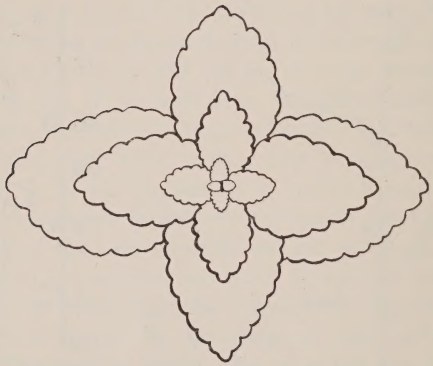

FIG. 47.—Leaf Mosaic of Dead-nettle.

The leaves are opposite and decussate, and are viewed from above. They are so arranged that the minimum amount of interference with the passage of light occurs.

usually correlated with the response of the plant to external conditions, especially to those of illumination.

MODIFICATIONS OF LEAVES OR PARTS OF LEAVES

The usual functions of the leaf are transpiration, photosynthesis and respiration, but sometimes a leaf, or a portion, may serve some other purpose. This special use of the leaf may not interfere with its ordinary work, but usually it does, and then some method of compensation for the interference is adopted. The special use of the first leaves or cotyledons to serve as food-reservoirs, and the reduction of leaves to

scales on buds and underground structures, have already been mentioned. Other modifications occur in which the whole leaf, or a part of it, serves as a means of climbing, or as a protection against browsing animals, or as an insect-trap.

Climbing Agents. Leaflet-tendrils are found in the vetch, pea, etc., some of the leaflets in a compound leaf being changed into tendrils (Figs. 48, 49).

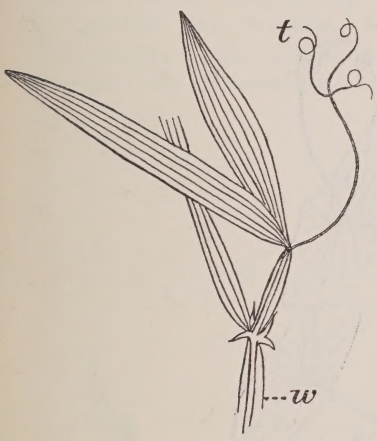

FIG. 48.—Leaflet-tendril of Wild Pea (*Lathyrus sylvestris*).

The stipules remain small, but the stem has become winged so as to compensate for the loss of leaf-surface. *w*, wing; *t*, tendril.

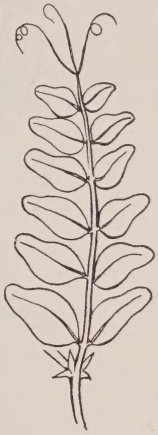

FIG. 49. — Leaflet-tendrils of Bush Vetch (*Vicia sepium*).

Only a few leaflets have become modified into tendrils and there is no need for the stipules to become large or the stem winged; possibly the leaflets are larger than they were before modification occurred.

Leaf-tendrils. These occur in the leafless vetch (*Lathyrus aphaca*) where the whole leaf forms the tendril (Fig. 50). In this case the stipules become much enlarged, and compensate for the loss of normal leaf-surface. This method of compensation can be shown in other members of the vetch family when part of the leaf only has been changed into a tendril, though sometimes the stem becomes broadened by a wing, as in the sweet pea. The examination of a number of different kinds of vetches and peas illustrates the principle

FIG. 50.—Leaf-tendril of Leafless Vetch (*Lathyrus aphaca*).

The whole leaf has been changed into a tendril, and enlarged stipules compensate for loss of leaf-surface.

of compensation very well, and also shows that the amount of extra leaf-like surface formed is more or less proportional

to the amount of leaf surface lost. **Stipule-tendrils** are found in the sarsaparilla (*Smilax*), the tendrils being formed from stipules. In the old man's beard (*Clematis*) the petioles of the compound leaves twist round the surrounding shrubs and are called **petiole tendrils or climbing petioles** (Fig. 51).

Leaf spines. A spine may be formed by a tooth of the leaf on the margin (e.g. holly) or the whole leaf may be changed into a spine. In the barberry (Fig. 52), the three-pronged spine has no leaf below it, and in its axil is a shoot with crowded leaves, so that it must be an altered

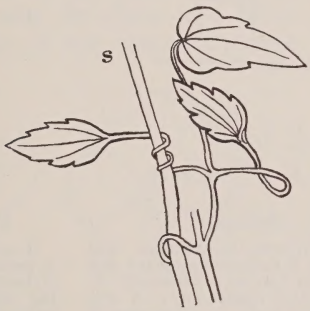

FIG. 51.—Climbing Petioles of Old-man's-beard (*Clematis vitalba*).

The leaves are opposite and usually have three leaflets. Only one of the leaves is shown, and the stalk of one of its leaflets is twining round the support (*s*).

leaf. In the gorse (Fig. 52) the spines are chiefly formed by stem structures, but some are formed from the leaves. **Stipule spines** (Figs. 30, 41) are formed in some acacias, and also in the false acacia (*Robinia pseudacacia*).

Insect-traps. In some plants the leaf, or part of it, is modified into a structure by which insect-food is obtained by the plant, and these plants will be dealt with in Chapter XIX.

Bracts. The leaves in whose axils the flowers arise are known as bracts. They may be similar to ordinary foliage-leaves, or they may have a different size and shape (Figs.

53, 68, 73, 145) and are often useful as a protection to the infant flowers. In some cases the leaf is modified to serve as a sheath or **spathe** for a group of flowers, as in the cuckoo-pint (Fig. 87).

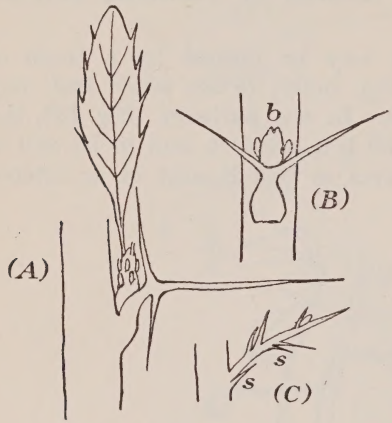

FIG. 52.—Spines.

A, leaf-spine of barberry with three prongs. The short branch in the axil is somewhat extended and all the leaves except one have been pulled off. *B*, younger leaf-spine with two prongs only; *b*, bud in the axil with secondary buds. *C*, stem-spines of gorse in axils of small leaves (*s*). A bud is present in the axil of one leaf.

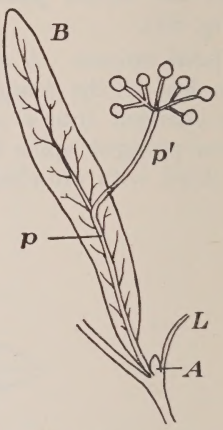

FIG. 53.—Lime.

A, accessory bud; *B*, bract; *p*, peduncle attached to bract; *p'*, free portion of peduncle bearing dichasial inflorescence; *l*, leaf-stalk.

Floral Leaves. The flower has some parts which are leaf-like, and may correspond to leaves. These will be considered in Chapters VIII and XVIII.

CHAPTER VIII

THE FLOWER

We all think that we know what a flower is, but our knowledge may not be so profound as we imagine. Before we attempt to give any definition of a flower, we will examine the flower of one of our common plants.

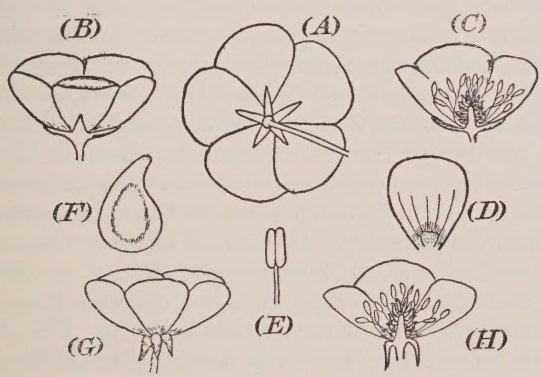

FIG. 54.—Flower of Buttercup.

A, creeping buttercup (*Ranunculus repens*), viewed from below, showing the stalk or pedicel, 5 sepals and 5 petals. *B*, side-view. *C*, view of flower cut in two. In addition to the sepals and petals, stamens and carpels are shown on the swollen top (thalamus) of flower stalk. *C*, *D*, single petal with nectary at base. *E*, stamen. *F*, carpel with the position of ovule indicated. *G*, bulbous buttercup (*R. bulbosus*) showing 3 out of 5 reflexed sepals. *H*, vertical section.

The Buttercup

The flower of a buttercup (Fig. 54) is a convenient one to examine during any part of the summer, and may be taken as our type. It has a stalk (*pedicel*) which becomes thicker

where the flower-parts come off and this portion is called the *thalamus*. The outer parts of the flower are five little green leaves (*sepals*) enclosing five larger yellow leafy bodies (*petals*); within these we get a number of yellow-knobbed bodies (*stamens*), and right in the centre are a number of little greenish oval bodies (*carpels*). We have thus four groups or rings (*whorls*) of different bodies, (1) a cup or *calyx* of five green sepals, (2) a *corolla* of five yellow petals, (3) an *andrecium* of an indefinite number of stamens, and (4) a *gynecium* or *pistil* of an indefinite number of carpels. Each of these whorls has its particular work to do in helping to form the seed, which we all know is the ultimate result of the flower. Some of the flowers will probably have gone to seed, and we can see that the seed-boxes (fruits as the botanist calls them) are formed from the carpels, which therefore seem to be the most essential parts of the flower, and, so far as we can judge from a superficial examination, the only bodies which are necessary, since the sepals, petals and stamens drop off whilst the carpels get larger and become the seed-boxes or fruits. This, however, is not the case, for if we cut off the stamens from a number of flowers, and enclose them in little bags or boxes so that neither insects nor wind can carry anything from the stamens of other flowers to them, the carpels will not develop their seeds. If a small brush, such as artists use, is rubbed against the ripe stamens of an uninjured flower, and then rubbed against the carpels of an injured flower, the carpels will then produce seeds. The stamens, then, are essential parts of the flower. The cutting off of the sepals and petals may have little effect on the formation of seed, and therefore they are not exactly necessary to what a botanist considers to be a flower, though we shall see that they do very useful work in helping the process of seed-formation.

Pistil. At the base of each carpel is a swollen portion which is called the *ovary*, since it contains the *ovule* or undeveloped seed, whilst at the top is a little knob (*stigma*) which is somewhat sticky in order to catch the yellow dust which comes from the stamens. In many plants, an intermediate

portion (*style*) connecting the stigma with the ovary is well developed, but in the buttercup it is very short, the stigma being almost directly on the ovary.

Stamen. Each stamen consists of a slender stalk (*filament*) bearing a knob (*anther*) at its apex. The anther is divided into two anther-lobes, and, when ripe, contains a quantity of yellow dust or *pollen*. It is this pollen which is necessary for the seed-formation in the carpels. It may be carried about by wind, insects, or other means and no doubt we have often assisted the process when walking through a field of buttercups.

Pollination. Insects are the chief agents for the work of pollination, i.e. taking the pollen to the stigma. As they come to the flower to obtain honey, they incidentally get some of the pollen on their bodies, and this is deposited on the stigma of the same or another flower. It is better for the flower to be a different one, or better still, to be one from a different plant. Many experiments have been tried at various times and the results show that better seed is obtained if the pollen is brought from the flower of one plant to the stigma in the flower of another (*cross-pollination*).

The *honey-bag* or *nectary* in the buttercup-flower is at the base of the petal, and the honey[1] which distils into it, is sometimes so copious as to be detected by the tip of the tongue. The petal of the buttercup may then be regarded as the honey-carrier, but it is more likely that it serves as a sign to the insects who associate bright petals with the presence of honey. The scent of the flower may also assist the insect in its search for honey. Another function of the petal is that of protection for the essential parts of the flower, though the calyx sepals are the chief bodies which keep off cold and wet from the more delicate parts, most of us being familiar with the way in which flowers close up when the weather is unfavourable. This is well shown by the earliest buttercup of the springtime, the lesser celandine. When the sun is shining, the bank is gay with the yellow-petalled flowers,

[1] Technically this fluid is not honey but the sugary liquid (nectar) from which the bee manufactures honey.

but, if the sky becomes overcast, and rain or cold intervenes, the green sepals wrap round the petals and, though hiding their beauty, enable them to withstand the inclement conditions.

The Bramble

The flower of the bramble will be found to be very similar to that of the buttercup, though the stamens are less definitely fixed on the top of the thalamus but appear to be fastened to the bases of the sepals.

The Sweet Pea

The flower of the sweet pea (or a similar flower, such as that of the laburnum or vetch) reveals a slightly different

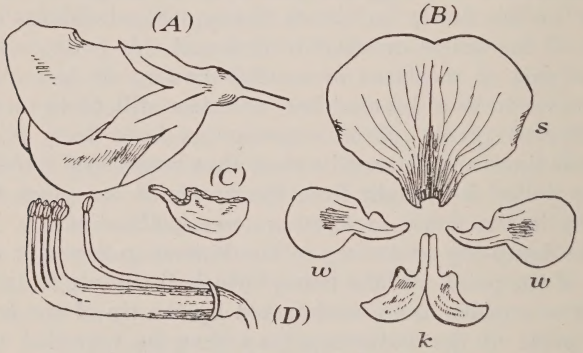

FIG. 55.—Flower of the Pea.

A, side view showing the gamosepalous calyx and three of the petals. *B*, the petals in natural position, but spread out. *k*, keel; *s*, standard; *w*, wings; *C*, keel, in its natural condition. *D*, inner portion of flower, the sepals and petals having been cut away.

structure from that of the buttercup. The sepals are still five in number (Fig. 55), but they are joined together (**gamosepalous**) at their bases to form a more definite cup, thus preventing marauding insects obtaining honey from the base of the flower. The petals, though their number is the same as in the buttercup, are very different in appearance. One petal at the back is the largest and most prominent, and is termed the standard; two petals at the sides are called wings and two petals in front are partly joined together to

form a keel. The stamens are ten in number, nine having their filaments united, the remaining one being separate, so that there are two groups of stamens and they are therefore said to be **diadelphous**. The pistil (Fig. 56) consists of one carpel only ; the ovary is long and the style is well developed.

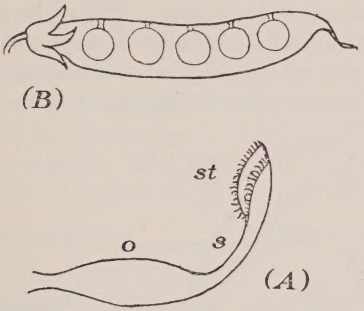

FIG. 56.—Pea.

A, pistil ; *o*, ovary ; *s*, style ; *st*, stigma. *B*, fruit (legume) ; the persistent calyx is shown at the base, the remains of the style and stigma at the apex, and the positions and attachments of the seeds are indicated (optical section).

The Snapdragon

All the flowers we have hitherto examined had their petals separate from each other (**polypetalous**), but in many flowers the petals are joined together, and the corolla is then said to be **gamopetalous.** The snapdragon (*Antirrhinum*) is a suitable gamopetalous flower (Fig. 57) to examine. The five sepals are slightly gamosepalous and the petals join together to form a two-lipped corolla. The upper lip has two lobes, and the lower one three, and as there are five lobes altogether we may conclude that the corolla consists of five petals. The lips are so arranged that only certain kinds of insects are able to reach the honey at the base of the corolla-tube. The stamens grow up with the corolla, so that the filaments are fastened to the corolla-tube, and the stamens are then said to be **epipetalous.** As there are five sepals and five petals we should naturally expect to find five stamens at least, but there are only four present, the posterior one being missing.

The position which would have been occupied by the fifth stamen is now occupied by the style and stigma, so that we may assume that the suppression of the fifth stamen has something to do with the method of pollination. There are only two carpels, but instead of being separate (**apocarpous**), as in the buttercup, they are joined together (**syncarpous**), so that only one ovary is present. The styles are so intimately joined that no trace of their fusion is apparent, but the stigma shows some trace of its original twofold nature by a slight furrow. This syncarpous arrangement is an economical one,

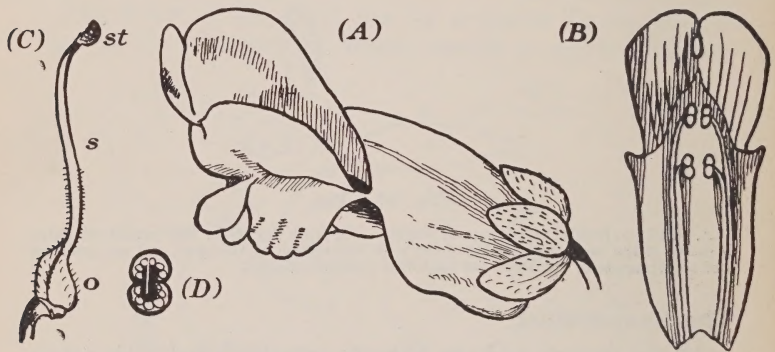

FIG. 57.—Snapdragon.

A, side view of flower showing the two-lipped gamosepalous corolla. *B*, posterior petals (upper lip) and the four epipetalous, didynamous stamens. *C*, pistil; *o*, ovary; *s*, style; *st*, stigma. *D*, a somewhat oblique (theoretically transverse) section of ovary showing the two carpels and the seeds arranged on an axile placenta.

since less material is required to form a two-chambered ovary than to form two separate ovaries having the same capacity.

In the Snapdragon the position of the pistil, relative to the other parts of the flower, is similar to that in the buttercup. Both these flowers are said to be **hypogynous**, since the sepals, petals and stamens originate below the gynecium. In some plants (e.g. willow-herb and narcissus) the ovary seems to be below the rest of the flower-parts, and then the flower is **epigynous**. An intermediate and rather indefinite relative position of the parts gives a **perigynous** flower. The bramble and the pea are examples of perigynous flowers,

though the perigyny is slight in both cases. A better example of a perigynous flower is shown in the apple, in which the ovaries fit in a concave thalamus. In perigynous flowers the stamens often appear to be fastened to the sepals, and the thalamus is usually more concave than in hypogynous flowers ; in fact, the concavity of the thalamus is so deep in some flowers (e.g. rose) that they are almost epigynous.

Regular and Irregular Flowers. The floral-leaves of the buttercup and bramble are arranged in a symmetrical manner, and their flowers are said to be regular. In the pea and snapdragon, little symmetry is shown, and their flowers are termed irregular ones. The symmetry of flowers will be further considered in Chapter XXI.

Flower of Monocotyledon

The buttercup, bramble, pea and snapdragon are all dicotyledons with fairly showy flowers, and their examination ought to be supplemented by that of other types. The flower of the lily (or tulip or bluebell, Fig. 141) may be examined as a type of the flower of a monocotyledon, as it is fairly easy to understand. There are three sepals and three petals but the three sepals are little different from the petals in appearance, and are only called sepals because of their outer position. This difficulty is often avoided by discarding the terms calyx and corolla, the six segments being called a **perianth.** There are two whorls of three stamens each, and the syncarpous pistil consists of three carpels. The number of carpels is shown by the three stigmas being quite distinct, and also by a cross-section of the ovary revealing three chambers.

Incomplete Flower. The vernal starwort (Fig. 58) is such a common plant in our ditches that it is very convenient to examine as an example of an incomplete flower, or a flower which possesses the essential portions, but has some or all of the protective envelopes missing. The plant has two different kinds of flowers, which are minute and borne in the axils of the upper leaves. The staminate flower consists of one yellow stamen, which rises just above the surface of the water,

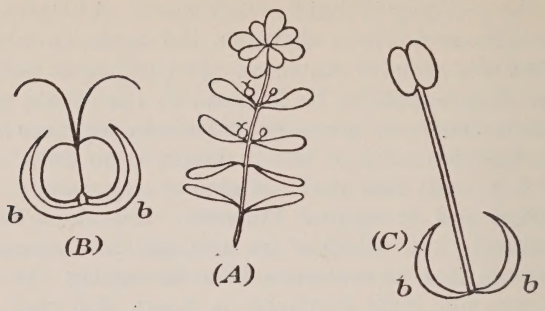

FIG. 58.—Vernal Starwort, showing the rosette and floating leaves and narrower submerged ones.

Staminate and pistillate flowers (exaggerated in size) are shown in the axils of some of the leaves. *B*, pistillate flower (× 6). *C*, staminate flower (× 4). *b*, bract.

and can be seen with the naked eye. The pistillate flower is not easily seen, as it is usually below the surface of the water, and consists only of an ovary with two stigmas at the top. Both the staminate and pistillate flowers are very much reduced; no perianth is present but usually two little bracts are found at the base of the stamen, or ovary, as the case may be. Flowers like these, which contain one kind of sexual organ only, are said to be **unisexual**. The vernal starwort is **monoecious** (meaning one-housed) as the staminate and pistillate flowers are on the same plant. Another example of a monoecious plant is the duckweed (Fig. 16), in which the flowers are still further reduced.

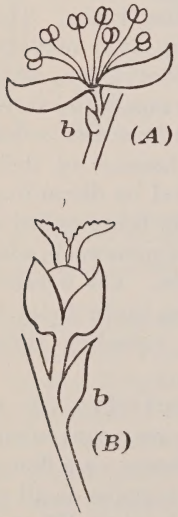

FIG. 59.—Dog's Mercury.

A, staminate flower. *B*, pistillate flower from a different plant. *b*, bract.

Dog's mercury has its two kinds of unisexual flowers on different plants (Fig. 59), and is said to be **dioecious** or two-housed. A flower which contains both stamens and carpels is said to be perfect or **hermaphrodite.**

Homologies of the Different Parts of the Flower. When an organ of a plant is altered so as to serve a different purpose than its usual one, we say that the altered organ is homologous with the original one. The tendrils of the ivy are homologous with roots, those of the vetch are homologous with leaflets, whilst the homology of a vine tendril is with a stem. Are the sepals, petals, stamens and carpels organs in their own right, or are they homologous with some other kind of organ? The examination of a number of flowers leads us to the view that the floral parts are homologous with leaves. The sepals are often very much like little leaves, in fact in some plants it is not easy to distinguish between sepals and bracts (e.g. jessamine and some anemones). Then, one occasionally finds a flower in which the sepals have varied from their normal appearances, having become similar to the foliage leaves both in size and shape (Fig. 60). Such sports are not uncommon in some flowers (e.g. cranes-bill), and show that a sepal is able to form a leaf when the conditions are suitable. As our acquaintanceship with flowers increases, so will the evidence for the homology of a sepal with a leaf increase. Sepals and petals are usually quite different in appearance, especially in regard to colour, but there are so many flowers in which there is little or no difference in the shape, size or colour of the petals and sepals, that we are forced to conclude that both are corresponding structures. There is more difficulty in obtaining evidence to show that a stamen or carpel is homologous with a leaf, but careful examination of some flowers (e.g. tulip, Fig. 61, *B*) will reveal cases of stamens changing into petals, though we must regard their pollen-containing boxes (**pollen-sacs**) as structures which are absent from ordinary leaves.

FIG. 60. — "Jack-in-the-green" Primrose.
The sepals have become leaflike.

Double flowers often have no stamens or carpels, all

these structures having been changed into petals. In the double carnation the stamens have not only become altered into petals, but they have also divided, so as to further increase the number of petal-like bodies. In the double cherry, the pistil is represented by green leaves, and in many other cases of doubling, the additional petals can be shown to represent stamens or carpels (Fig. 61).

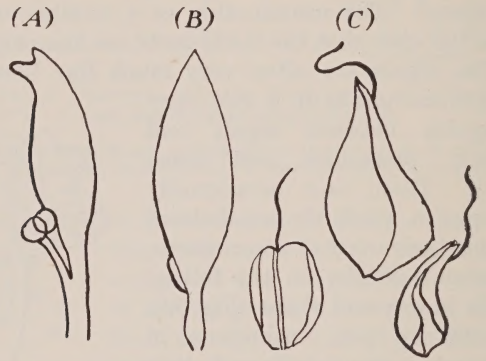

FIG. 61.—Alterations of Stamens and Carpels into Petaloid or Sepaloid Structures.

A, postero-lateral stamen of *Polygonum persicaria*, showing chorisis and metamorphosis of anther-lobe into petal: the stamen has divided into two parts; one part has two pollen-sacs, the other has become petaloid. *B*, stamen of tulip changing into a petal: one anther lobe is little altered, the other has become petaloid. *C*, three changing carpels, from an abnormal flower of the greater stitchwort, all the floral parts of which were sepaloid. The carpels were not syncarpous as in the normal flower, but free from one another; the styles were distinct, but the lower portions were sepaloid.

Evolution of Floral Leaves. Although we must regard the evidence as sufficient to establish the homology of the floral parts with leaves, it does not follow that sepals, and the vegetative portions of stamens and carpels are modified leaves or that they are derived from leaves. The evidence merely establishes the homology, and may justify the opposite view that leaves have been derived from the stamens and carpels, or from the cases surrounding the pollen-sacs and ovules. Our evidence only warrants us to say that foliage and floral leaves have a common origin, and a study of the lower forms of plant-life may possibly lead us to the theory

that foliage-leaves have been derived from the expansion of the bodies containing the reproductive organs.

Other Floral Types. In addition to the flowers which have been dealt with in this chapter further examples for study are given in Chapter XX. The next flower we should examine is that of the dandelion. There are so many points of interest about this plant that it will be considered in a separate chapter.

CHAPTER IX

THE DANDELION

This common weed of cultivation was called dent-de-lion by the Normans because its leaves had teeth which resembled those of the lion, and our English name is merely a corruption of this earlier one. The examination of its so-called flower (Fig. 62, *A*) soon lands us into difficulties. At first, we are inclined to regard the green bodies on the outside as an indefinite number of sepals, and the yellow bodies further in as petals. We would then expect the carpels to occupy the centre, whilst the stamens would be in an intermediate position, but we find that nothing of the sort occurs. The carpels appear to be scattered amongst the petals, and a superficial examination reveals no stamens. The way in which the carpels are scattered suggests that we are not dealing with a single flower, but that a number of flowers are bunched together, and if we carefully examine the " flower " according to this theory we soon find abundant evidence to confirm the theory.

Each of the apparent petals is really a corolla (Fig. 62, *B*), which is strap-shaped at the top and narrows downwards so as to form a slender tube at the base. As there are five little teeth at the top of the corolla, we may consider that it is a gamopetalous one, consisting of five petals. Below the corolla there is a little cylindrical ovary, and from the top of this, the style continues up the corolla-tube, and, after emerging from it, divides into two stigmas. Just at the place where the petals form a tube, five little stalks can be seen attached to the tube. These seem to join together to form a tube round the style, and as pollen-grains can be

obtained from this tube, it must consist of anthers, which have joined together or become **syngenesious.** The five teeth at the top, the five marks on the outside and the five stalks indicate that there are five stamens (Fig. 62, *C*), which are epipetalous, since the filaments are attached to the corolla. There are no sepals present, and if there were, one can scarcely imagine that they would be of any use to the

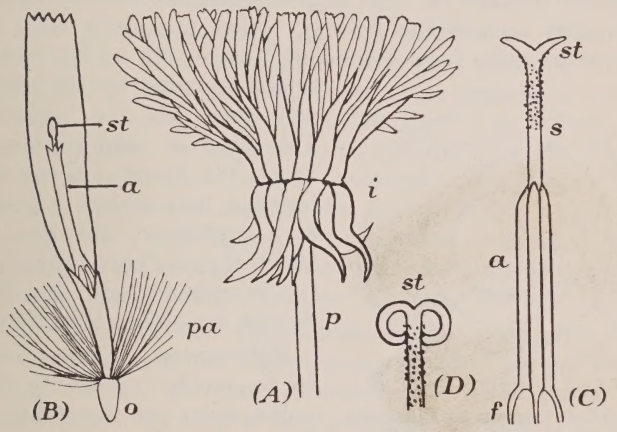

FIG. 62.—Dandelion.

A, inflorescence. *B*, single flower. *C*, stamen with separate filaments (only 3 out of 5 shown) and syngenesious anthers enclosing the style which divides at the top into two stigmas. Below the stigma, the style is dusted with pollen. *D*, top of pistil in which the stigmas have turned back so that self-pollination may occur. *a*, anthers; *i*, involucre of bracts, the lower ones being reflexed; *o*, ovary; *p*, peduncle; *pa*, pappus; *s*, style; *st*, stigma.

flower; they would merely be relics of a simpler form of flower. A number of hairs (**pappus**) are noticeable just where we should expect to find the sepals, and it seems reasonable to conclude that this pappus of hairs has been derived from the calyx. We all know that this pappus is useful for distributing the fruits later on. The flower of the dandelion then is an epigynous one, and consists of a calyx modified into a pappus, a gamopetalous corolla of five petals, an andrecium of five syngenesious, epipetalous stamens and a syncarpous, bicarpellary (the two carpels are indicated by

the two stigmas) pistil with an inferior ovary, a long style and two stigmas (Fig. 62, *C*).

Economy in Aggregation of Flowers. The crowding of the flowers economizes the material required to form the envelopes for protection and conspicuousness, the whole flower-head (**inflorescence**) being protected, not only in bud but also later on, by the bracts which form a ring or an involucre beneath it. The upper bracts are usually closely imbricated around the flowers, whilst the lower ones are reflexed so as to form a kind of "maze," in which insects, trying to enter by the wrong way, are lost or impeded. This kind of inflorescence in which the flowers are crowded together into a head is known as a capitulum, the disc on which they are borne is termed the receptacle, and the little flowers are often called florets.

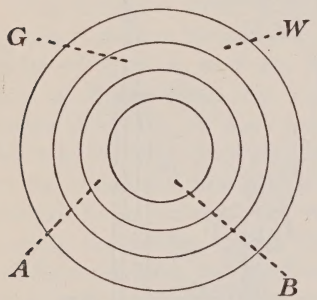

FIG. 63.—Diagram to Illustrate Ripening of Flowers in Capitulum of Dandelion.

A, ripe stamens and unripe stigmas; *B*, florets in bud, neither stigmas nor stamens ripe; *G*, ripe stigmas and withering stamens; *W*, withering florets.

Pollination. There seems to be much probability that pollen from one floret will be deposited on the stigma of a neighbour, but a careful examination of the inflorescence shows us that **cross-pollination** is the rule when a sufficient number of insects are on the wing. An inflorescence which has been flowering for some time shows unopened florets in the centre (Fig. 63); then a ring of florets with ripe stamens, and unripe, undivided stigmas; then a ring of florets with more or less withered stamens and ripe, divided stigmas, whilst the outermost florets may be withered and forming fruits. An insect visits the outer florets first, works towards the centre and then flies away to another inflorescence. Assuming that it has brought pollen from another plant, it will deposit this foreign pollen on the ripe stigmas in the outer rings, and then proceed towards the inner florets, where it will get dusted

with pollen to carry to another inflorescence. The unripe stigmas are at first unopened, and are below the top of the tube formed by the united (syngenesious) anthers, which split towards the inside of the tube. As the style lengthens, the pollen is pushed up by the unripe stigmas, which thus act as **pollen-presenters** to the visiting insect. Later on, when the stigmas spread out, any pollen not carried away by insects will be on the under sides, and therefore ineffective, since the upper surfaces are the only portions on which the pollen can act. When cross-pollination does not occur owing to the scarcity of insects, or for some other reason, the pollen remaining on the upper part of the style may be utilized for **self-pollination,** the stigmas curling round (Fig. 62, *D*) till their receptive surfaces come in contact with the style. This method is frequently adopted by flowers which appear in the early or late months or under any other conditions, when insect visitors are scarce. The curling of the stigmas may also occur even when cross-pollination has been effected.

Movements of the Capitulum. After pollination the capitulum becomes less conspicuous, till the "clock" stage appears. During the interval between the withering of the florets and the ripening of the fruits, the inflorescence stalk (**peduncle**) bends down, and therefore the developing fruits are exposed to less extreme atmospheric changes and the capitulum is less liable to hold water. A similar position is occupied by the capitulum before the florets open, the erect habit being maintained only at the times when there is most need of it, when the flowers must exhibit themselves to attract the pollinating insects, and when the fruits must be in the best position for the wind to catch the pappus in order to blow the fruit away. The fruit (Fig. 64, *A*) is admirably fitted for wind-dispersal, and only contains one seed, though the two carpels might lead us to assume that at least two seeds would be formed.

Nyctitrophism. Another movement shown by the dandelion is the "sleep" movement (nyctitrophism). During the day the inflorescence is expanded, but when twilight approaches it closes up, the florets becoming erect, and some-

what twisted, so that only the tips of the corollas are exposed. Such nyctitrophic movements are exhibited by many other flowers, though they are perhaps best shown in the dandelion and its allies. In the goatsbeard, the capitulum closes early in the day, the heat of the afternoon sun is avoided and so the plant is sometimes known as John-go-to-bed-at-noon. In some plants (e.g. evening primrose, night campion), which are pollinated by twilight-flying moths, the flowers are closed during the day and open when evening approaches. Similar nyctitrophic movements are exhibited by the leaves of the wood-sorrel, clovers and many other plants, and serve as protective devices against conditions unfavourable to the plant.

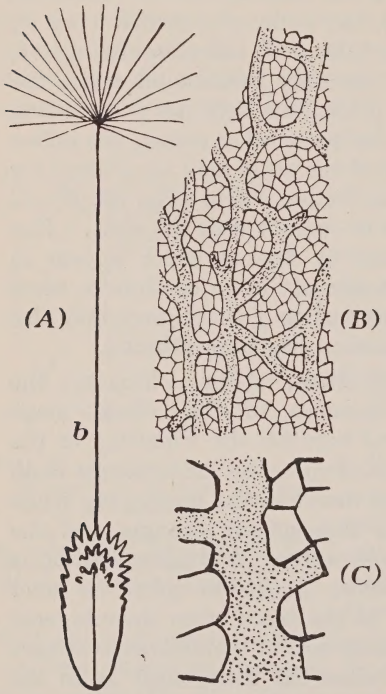

FIG. 64.—Dandelion.

A, fruit (cypsela) (× 7). *b*, beak. *B*, portion of L.S. of root (× 40): laticiferous cells are dotted. *C*, small portion of *B* (× 200).

Owing to its economical method of pollination, and its effective apparatus for seed-dispersal, the dandelion is a common plant, though these characters are not the only ones by which it is enabled to compete against its neighbours. Two other characters possessed by it are excellent auxiliaries; it has a long tap-root, often over a foot long, and therefore during periods of drought can obtain water from lower strata of the soil than its neighbours; its leaves are arranged in the form of a rosette, which crowd out any small com-

petitors, so that the plant monopolizes a greater area.

Latex. During our examination of the dandelion, the milky juice, which exudes when the flower stalk or any other part is broken, must have been noticed. This milky juice is known as latex, and is present in many other plants (cat's-ear, sow-thistle, hawksbit), which are akin to the dandelion, and, in fact, are often mistaken for small dandelions. This latex is contained in tubes (Fig. 64), which consists of cells joined together. In the dandelion it may possibly be of use in preventing some animals from eating the leaves, but it is better regarded as an excretory substance. Plants, like animals, produce waste substance as a result of their activities, and, if these cannot be got rid of in the form of gas, they must usually remain in the plant. An accumulation of such substances will interfere with the activities of the plant, unless they are stored away or otherwise disposed of, so that they do not interfere with the active cells of the plant.

In the dandelion and its allies, the latex is contained in a branched system of tubes formed by cells joining together (Fig. 64, *B* and *C*). Such **laticiferous** (latex-containing) vessels are known as **laticiferous syncytes.**[1] In the spurges, the laticiferous vessels also form a branched system of tubes, but in these plants each vessel begins as a single cell which continues growing and branching in an indefinite manner. Such vessels are termed **laticiferous cœnocytes,** and frequently contain starch-grains of a peculiar dumb-bell shape (Fig. 78, *F*). In many other plants, the latex is stored away in single cells (Fig. 80).

Many substances are found in these laticiferous vessels and cells. Resinous and other incompletely oxidized substances are often present. In the latex of *Hevea* and some other plants, a rubbery substance is present in sufficient quantity to enable its extraction and preparation to be a profitable transaction. From the latex of the poppy, and especially from that of the opium poppy, opium is obtained. In most cases, the latex

[1] The distinctions between syncytes and cœnocytes and later remarks on the mechanics of the plant will be better appreciated after Chapter XII has been studied.

is of a white colour, but in the banana it is colourless, and in the greater celandine it is yellow.

Tensions in Plant-structures. The inflorescence stalk of the dandelion is also useful for studying the mechanics of the plant. Herbaceous plants owe their rigidity largely to the manner in which their cells are pressed together. When the cells are swollen with water the stalk is erect, but when the water escapes more quickly than it is taken up, the plant becomes limp. The flagging or wilting of plants is very noticeable on a hot summer's day, when transpiration is in excess of absorption. If the cells on one side only are distended with water, that side will be the longer one, and the plant structure will become curved. In the following experiments some idea of the tensions occurring in plant-structures may be obtained.

Experiment 37. To show longitudinal tension in a stem structure. Take a measured length (about 20 cm.) of the petiole of a rhubarb plant, and dissect, so as to obtain strips of the outside (epidermis), intermediate (cortex) and internal tissues (pith). Measure each, immerse in water and measure again. Immerse in salt solution (6 per cent.), and measure again. Treat a young peduncle (stalk on which the flower-head is borne) of the dandelion similarly. Note that the outer tissues are shorter than the inner and that osmosis occurs much more quickly with the cells of the inner tissues. In a particular experiment with the rhubarb, the following results were obtained :—

		After water.	After salt solution.
Length of petiole	21·9		
,, ,, epidermal tissue . .	21·6	21·6	21·3
,, ,, cortical tissue . .	22·1	22·7	22
,, ,, internal tissue . .	22·8	26·2	23·5

Experiment 38. To show that there is transverse tension in a woody stem. Cut two rings through a privet-stem, one ring being about 3 mm. below the other. Join the two transverse cuts by a longitudinal slit and carefully peel off the bark. Try to replace the bark so as to hide the exposed wood.

CHAPTER X

THE FRUIT AND SEED-DISPERSAL

Pollination refers to the carrying of the pollen from the stamen to the stigma, but, after this, much remains to be done before seed is formed. Something from the pollen-grain must, in some way or other, be carried down the style to the ovule in the ovary. As the result of this action, which we call fertilization, the ovule becomes a seed and the ovary a seed-box or fruit. When the ovary contains more than one ovule, the same process occurs for each of the ovules, so that as many pollen-grains are required as there are seeds in the fruit. Most people, when they speak of a fruit, mean a seed-box which can be eaten, but botanists use the term in a much wider sense. As a result of changes which occur after fertilization, the ovules develop into seeds, and the ovary swells out to form what botanists term the **fruit**, whether it is eatable or not. Sometimes other parts around the ovary are also stimulated to further growth. When this occurs, the whole structure may be called a false fruit (**pseudocarp**) and the true fruit or fruits are enclosed within it or scattered on the surface. In the apple, pear, medlar and similar "fruits" the top of the thalamus becomes juicy, and grows round the core containing the true fruits (Fig. 66). In the strawberry, the top of the thalamus also becomes juicy, but the true fruits are not enclosed, but form the so-called "seeds" on the outside.

We may classify fruits into two main groups. The first group contains those which are juicy, and therefore reckoned by everybody as fruits. The second group consists of dry fruits, and many of them are called seeds by most people.

Juicy Fruits

Juicy fruits may be stony fruits, as in the plum and cherry (Fig. 65, *A*), or stoneless, as in the gooseberry. The stony fruits are called **drupes**, and in these, the covering or coverings (integuments) of the ovary have become changed into a fruit-wall, or *pericarp*, of three different parts. On the outside is a thin skin or *epicarp*, then comes the middle juicy portion or *mesocarp*, whilst the kernel or actual seed is enclosed in a hard stony portion or *endocarp*. The other kind of juicy fruit is known as a berry. This has a thin skin or

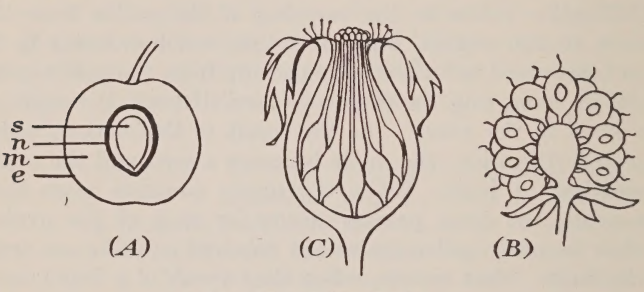

FIG. 65.—Juicy Fruits.

A, section of drupe of cherry. *e*, epicarp; *m*, mesocarp; *n*, endocarp; *s*, seed. *B*, section of aggregate fruit of bramble. Each little fruit is a drupe, has the same parts as a cherry, and is surmounted by the remains of the stigma. *C*, hip of rose. Five of the true fruits developing are shown enclosed in the concave thalamus, crowned by the leafy sepals. For the sake of clearness, the hairs on the fruits are not indicated.

epicarp on the outside, but there is no endocarp, the seeds being scattered in the juicy mesocarp. The grape is a berry because the little hard bodies inside are seeds. Other familiar examples of berry are snowberry, whortleberry, red and black currant, tomato, date, pomegranate, cucumber and orange. Some of these are rather peculiar in some respects, but they all agree in having an epicarp enclosing a juicy portion with seeds. The pomegranate has its seeds coated with a gummy substance; the orange, even when fully ripe, shows the number of carpels which formed it, whereas in most berries the divisions tend to disappear. The juicy kind of pseudocarp, in which the thalamus swells out to form a concave receptacle enclosing the ripening carpels, is some-

what similar to a berry, and is known as a **pome** (Fig. 66). In the apple and pear the number of carpels in the flower is five ; accordingly we should get five true fruits forming the hard core and enclosed by the juicy thalamus.

Berry. It must be noted that the popular term " berry " has no botanical value. The raspberry, blackberry and dewberry are not berries at all from the botanical standpoint. The carpels in the flower were numerous and separate from each other, and each one has given rise to a little fruit which

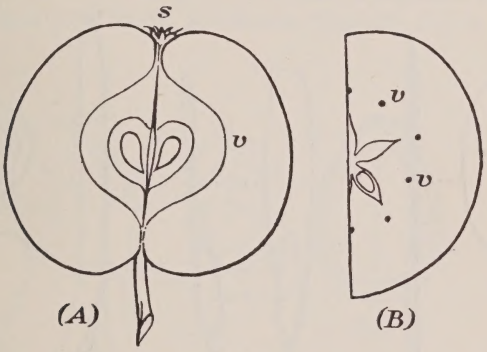

FIG. 66.—Apple.

A, L.S. of the pome : withered sepals (*s*) indicate that the juicy thalamus has grown round the true fruits. *B*, half of T.S. of pome. *v*, vein.

has the same kind of structure as a miniature cherry, so that these so-called berries are really collections of drupes. The strawberry is not a berry, but a false fruit in which the true fruits are the hard " seeds " fixed on the juicy portion formed by the growth and ripening of the thalamus.

Dry Fruits

These are much commoner than juicy ones, and may be arranged in three groups. In the first group of indehiscent or akenial fruits, the pericarp does not split open to let the seed out, so that before germination can occur, the pericarp must decay sufficiently to allow the developing seedling to push its way out. In the second group, dehiscent or capsular

fruits, the pericarp splits open to let the seeds escape, whilst in the third group (schizocarps), the pericarp does not split open to let the seeds out, but the fruit splits up into smaller fruitlets, each of which contains a seed and is enclosed in its own portion of the pericarp.

Akenial Fruits. Indehiscent or akenial fruits are usually formed from one carpel, and contain one seed only. The **akene** (e.g. buttercup (Fig. 67, *D*), avens, cinquefoil, barren strawberry) has a tough pericarp, whilst a **nut** (e.g. hazel

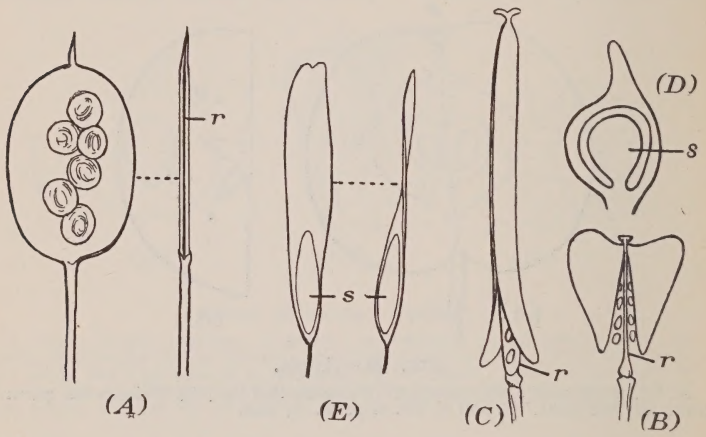

Fig. 67.—Dry Fruits.

A, silicula of honesty in front and side view. *r*, replum ; *B*, dehiscing silicula of shepherd's purse. *C*, siliqua of wallflower just beginning to open so as to expose the replum (*r*). *D*, akene of buttercup. *E*, samara of ash in front and side view. *s*, seed.

oak) has a much harder one (Fig. 68). In some akenes, the pericarp is drawn out to form a wing, and these winged akenes are known as *samaras* (e.g. ash (Fig. 67, *E*), elm). In the dandelion, hawkweed and similar plants, the akene is formed from an inferior ovary, and is usually surmounted by a ring (pappus) of hairs ; such an akene is sometimes distinguished as a **cypsela** (Fig. 64). It is formed from two carpels, and each carpel ought to contain its own seed, but normally only one ovule develops into a seed. In the maize, wheat, rice

and many other members of the grass family, the grain (Figs. 10, 11) is a fruit containing a single seed. As the testa is organically joined to the pericarp, the seed cannot be taken out; a fruit of this kind is called a **caryopsis.**

Dehiscent Fruits. The capsular fruits may be formed from one or many carpels, and vary in their method of splitting. When the fruit is formed from one carpel, and splits on one side only, it is called a **follicle** (e.g. marsh marigold (Fig. 69, *B*), columbine, monkshood), but when it splits on both sides, as in peas and beans, it is termed a **legume** (Fig. 69, *C*). The **siliqua** (e.g. stock, wallflower (Fig. 67, *C*)) is a capsular

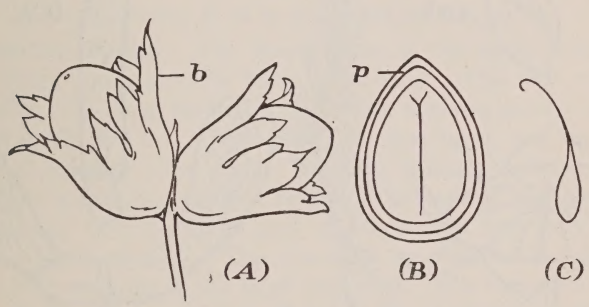

FIG. 68.

A, nuts and bracts of hazel. *B*, longitudinal section of nut. *C*, hooked akene of avens (× 3).

fruit formed from two carpels joined together, a false partition (*replum*) dividing the fruit into two separate chambers. The partition is said to be a false one, because it is not there when the ovary is young, but develops as the fruit ripens. When the siliqua is almost as broad as long, it is sometimes known as a *silicula* (e.g. honesty, pennycress, shepherd's-purse (Fig. 67, *B*)). During dehiscence or splitting, the pericarp divides into two longitudinal halves or valves, the seeds are often shot out, and the replum is left in the middle. In the garden plant known as honesty, the replums (Fig. 67, *A*) are large and silvery, and are used as ornaments. All other kinds of capsular fruits may be lumped together as capsules,

though we must realize that they vary very much in the number of parts, and in the method of dehiscence. A **capsule** may be formed from two carpels (e.g. snapdragon), or there may be three (e.g. violet), four (e.g. willow-herb), five (e.g. campion) or more (poppy) carpels (Fig. 71). It may allow the seeds to escape by means of pores, as in the porous capsule of the poppy, or by teeth, as in the campion, or the sides of the capsule may separate into valves, as in the willow-herb. In the scarlet pimpernel and henbane, the upper half of the

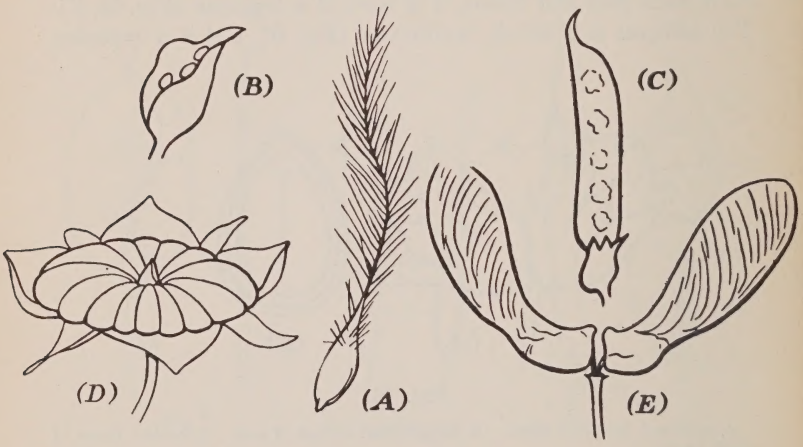

Fig. 69.

A, akene of clematis (× 3) with hairy style. *B*, follicle of marsh-marigold. *C*, legume of vetch. *D*, schizocarp of mallow. *E*, double samara of sycamore.

capsule falls off as a lid, and this kind of capsule is termed a *pyxidium* (Fig. 71).

Schizocarps. The dry fruits of the third group are the schizocarps or fruits which split up into smaller fruitlets, and these are very variable. In the maple and sycamore, the two fruitlets are winged akenes, and the whole fruit is therefore termed a double samara (Fig. 69, *E*). In the Indian cress (*Tropeolum*), the schizocarp consists of three parts, which, on drying, break away from one another. In

the families to which the deadnettle and borage belong, the fruit consists of a schizocarp which divides into four nutlets. In the cranesbill, there are five carpels forming a syncarpous ovary, and the schizocarp which results divides into five parts, whilst in the mallow, there are many carpels, and the resulting " flat cheeses " split up into many one-seeded fruitlets, each of which is like an akene (Fig. 69, *D*).

Aggregate Fruits. When the pistil is apocarpous and consists of many carpels, the fruits are crowded together, and the group of fruits is sometimes termed an aggregate fruit. In the buttercup, avens and cinquefoil, the aggregate fruit is a collection of akenes, whilst in the bramble, raspberry and cloudberry it is a collection of drupelets.

Peculiar Fruits. The pseudocarps of the apple and the strawberry have already been mentioned. The **hip** of the rose (Fig. 65, *C*) is formed in a similar manner to the pome of the apple, but less juicy material is developed, and the top does not entirely close over. The **haw** of the hawthorn does not differ materially from a pome. The walnut is a drupe ; the epicarp and mesocarp peel off when ripe, and leave the seed in the endocarp. The coco-nut, as sold in the shops, is the seed enclosed in the hard endocarp. The outer portions of the fruit, which are taken off before the coco-nut is exposed for sale, consist of a thin skin-like epicarp, and a middle portion of a fibrous nature. The fruit of the coco-nut appears to be a peculiar kind of drupe, in which the mesocarp is not juicy, but is fibrous in texture, and is able to be utilized in the formation of coco-nut matting. The berry of the ivy contains several seeds, each of which is enclosed in a firm investment, and therefore it may be termed a drupaceous berry. In the horse-chestnut, the " conkers " are the seeds, and are enclosed in a somewhat fleshy case. As the case splits open to let the seeds out, the fruit must be a kind of capsule with a fleshy pericarp, and may therefore be called a succulent capsule. The date has a juicy mesocarp, which surrounds a hard stony body, and may be mistaken for a drupe. The stone, however, is a seed, and the fruit must be considered as a one-seeded berry.

The fruits of the fig, mulberry, pine-apple, spinach and hop are partly developed from structures outside the ovary, and are therefore pseudocarps. In the spinach, the perianth forms a hard spinous envelope around the true fruit. In the **strobilus** of the hop, the true fruits or akenes are enclosed in the persistent and enlarged bracts of the pistillate inflorescence. In the mulberry, the fruit closely resembles the collection of drupes which is found in the bramble (Fig. 65, *B*), but the juicy portions are not formed from the walls of the ovary. In the bramble, the fruit is the production of a single flower, whereas in the mulberry the perianths of a group of flowers become juicy and enclose the akenes or true fruits. In the pine-apple a similar fleshy development occurs, and in addition the axis of the inflorescence becomes juicy.

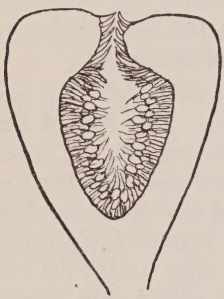

Fig. 70.—L.S. of Young Fig.

It is really an inflorescence with a concave thalamus and having a small opening (closed by bracts) through which pollination is effected (× 1½).

One of the most peculiar kinds of pseudocarp is that of the fig, the whole inflorescence contributing to its formation. The pistillate flowers are borne on the sides of a concave receptacle which has a pear-shaped form and is almost closed at the top (Fig. 70); they produce little akenes (the "seeds" of the fig), and the whole receptacle becomes juicy.

Naked Seeds. In the group of plants called Gymnosperms, to which the pine, yew and larch belong, there is no ovary, and consequently the seed is not enclosed in a fruit.

Dispersal of Fruits and Seeds

When the ripe seeds merely drop down on the ground near the parent plant, there will be competition with each other in regard to food, light, etc., and many, if not all, of the young seedlings will be unable to live. Many plants overcome this difficulty by having a method of scattering the

seeds, and then there is a possibility that they will fall into some position where germination and further development can occur. A plant which has some method of seed-dispersal has a much better chance of distribution than if that method was absent, though it does not follow that it has a better chance than another species which has no special means of seed-dispersal, since the distribution of a particular species of plant depends on other factors besides those of seed-dispersal. The methods of seed-dispersal adopted by different plants are very variable, but they may be roughly grouped under four agencies, namely: (A) wind, (B) animals, (C) water, (D) self.

(A) **Dispersal by Wind.** The seeds or seed-bearing bodies of some plants have large surfaces in relation to their weights, and are thus able to be blown away by the wind.

(1) *Winged fruits.* The fruits have wing-like outgrowths in the ash (Fig. 67, *E*) and elm.

(2) *Winged fruitlets.* In some schizocarpic fruits, the wings are on the margins of the fruitlets, as in the "keys" of maple and sycamore (Fig. 69, *E*), and in the two-seeded schizocarp of cow-parsnip and some other members of the family Umbelliferæ (Fig. 72, *B*).

(3) *Hairy fruits.* The dandelion, thistle and many other Compositæ have plumed fruits in which the plumes are formed from the modified calyx (Fig. 64), whilst in the clematis, the persistent style becomes hairy (Fig. 69, *A*).

(4) *Dry coverings.* Wings formed from the dried remains of flowers or leaves. In the dock, the fruit is covered with a winged calyx; in the hornbeam, hop and lime, dried bracts form the wings connected with the true fruits (Figs. 53 and 73, *B*).

(5) *Censer mechanism.* In the poppy, the capsule has a number of pores round the top (Fig. 71). When the wind blows, the fruit-stalk is bent, but when the force of the wind decreases, the resiliency of the stalk causes the fruit to swing back, and the seeds are shot out. In the campion, the same method is adopted, but the capsule opens by apical teeth. From a likeness to an acolyte swinging a censer this has been

termed censer mechanism. A similar method is adopted by some other plants in which the fruit is of a different kind.

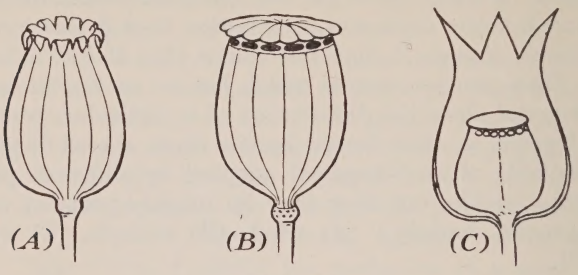

FIG. 71.

A, capsule of campion opening by ten teeth. *B*, porous capsule of poppy. *C*, pyxidium of henbane enclosed in the persistent calyx, half of which is cut away. (All × 1½.)

(6) *Small and light seeds.* In the orchids, the seeds are so minute, that when the capsule opens they can be readily blown about by the wind.

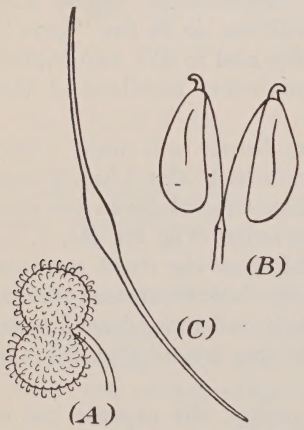

FIG. 72.

A, hooked fruit of cleavers (× 1½). *B*, cremocarp of fennel with two mericarps separating. *C*, seed of bog-asphodel.

(7) *Winged seeds.* In the stock the seed is somewhat flattened, and dispersal is thereby facilitated, but better examples of winged seeds are afforded by the pine (Fig. 171, *F*) and larch amongst British plants, and by the foreign plant *Bignonia*. In the bog-asphodel, the seed is drawn out at each end (Fig. 72, *C*).

(8) *Hairy seeds.* The seeds of the willow and willow-herb have a parachute mechanism (Fig. 74). During the ripening of the fruit, a tuft of hairs forms on each ovule, so that when the capsule opens the seeds can be blown about by the wind. Cotton is obtained from similar tufts of hairs on the seeds of the cotton plant.

(B) **Dispersal by Animals.** Many fruits form burs which stick to the clothing of animals, and are carried away. Others are of a juicy nature, and are eaten by animals, especially by birds. In many cases, the seeds are left, the juicy portion being pecked off, but in others the "seeds" are actually swallowed by the bird and pass right through it, their hard cases protecting them from the action of the digestive juices. In the hip of the rose, the juicy portion is formed from the top of the thalamus, which grows round and almost encloses the true fruits. Each akene is provided with hairs which irritate the throat of the bird, and so it is dropped. When

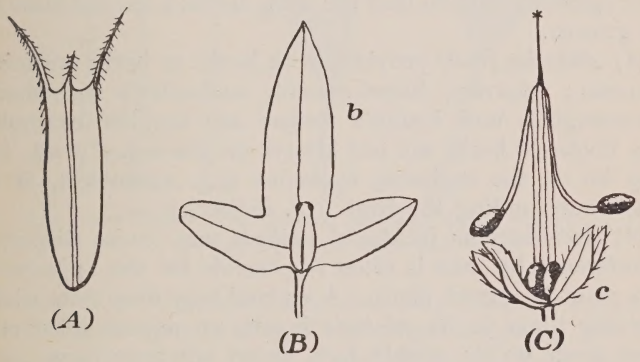

FIG. 73.

A, akene of bur-marigold (× 3). B, akene of bract on hornbeam (× ⅔). *C*, crane's-bill: schizocarp of 5 mericarps, two of which are shown breaking away from the central column (× 1½); *c*, persistent calyx.

the seeds pass right through the alimentary tract of the animal, a good supply of nutritious material is provided, and the development of a seed dispersed in this manner is more certain than if it had been dispersed by the wind. Generally speaking, a great deal more waste occurs in dispersal by wind than in dispersal by animals, as in the latter case a more suitable spot for development is more likely.

(1) *Juicy fruits with seeds enclosed in hard cases.* The juicy portion is eaten, and the stone dropped, in the cherry, plum, sloe, etc. The whole fruit is taken into the alimentary canal, but the endocarp protects the seed from the digestive

juices, in the raspberry and blackberry. In some cases, e.g. rose, mulberry, strawberry, the juicy coverings are formed by the thalamus or other structures outside the ovaries.

(2) *Juicy seeds.* During the ripening of the seed of the yew, an extra coat (**aril**), which encloses the seed except at the top, is formed. When the seed is ripe, this aril becomes red in colour and sweet in taste ; birds eat it and leave the hard and bitter seed.

(3) *Gummy seeds.* In the mistletoe, the seeds are surrounded by a sticky substance. The bird eats the juicy portion, and, in order to get rid of the sticky seeds, rubs its beak against a tree, so that the seeds are on a habitat suitable for growth.

(4) *Adhesive fruits* provided with hooks or barbs are fairly common ; cleavers, forget-me-not, enchanter's nightshade, bur-marigold, and hound's tongue are familiar examples. The hooks or barbs are not always on the actual fruit, but may be on the enclosing thalamus (e.g. agrimony), or on bracts surrounding the fruit (e.g. burdock).

(5) *Accidental or incidental methods* may cause dispersal. Interference by man is often responsible for the appearance of a plant in a fresh place. A squirrel may drop nuts whilst carrying them to its winter's hoard, an aquatic bird may carry seeds on its muddy feet, or an ant may leave gorse seeds in its tracks.

(C) **Dispersal by Water.** Plants which grow in or near a stream often have their seeds scattered by the running water. Some seeds are especially fitted for this method. The seeds of the water-lily are made buoyant, owing to the air-spaces in the spongy covering. The fibrous mesocarp of the coco-nut drupe enables it to float for long distances in the sea, though it is doubtful how far this is responsible for the seaboard distribution of the coco-nut palm.

(D) **Self-Dispersal.** When the siliqua of the bitter-cress is ripe, a slight touch causes the valves to roll up and the seeds are shot out with explosive violence. A similar explosive scattering of the seed is exhibited by the fruits of the violet, pansy and touch-me-not, though the details are slightly

different, for instance, the valves of the violet capsule close up and shoot the seeds out. In the Indian cress (*Tropeolum*) and cranesbill, the schizocarpic fruits split with some force and scatter the constituent fruitlets. The cranesbill also exhibits a hygroscopic method, by which the fruitlet may move some distance from the parent plant. Each fruitlet is provided with a long beak having a hook at the end, and

FIG. 74.—Willow-herb Capsule splitting into 4 valves ($\times \frac{2}{3}$).
The seed is provided with a hairy aril.

the length of this beak, like that of a fiddle-string, alters according to the humidity of the surrounding air. The hook fixes the fruitlet in position, and when the beak contracts the fruitlet is drawn on. When the beak gets longer, the weight of the fruitlet prevents a backward movement, and the hook is pushed out of the ground and forward. As soon as contraction begins to occur, the hook once more becomes fixed and the fruitlet drawn on, so that a slow movement of the fruitlet is effected.

CHAPTER XI

THE CHEMICAL COMPOSITION OF PLANTS

The following simple experiments should be performed in order to obtain a general idea of the composition of plants.

Analysis.—EXPERIMENT 39. To show the percentage of water in plants. Take some fresh leaves or other parts of plants, weigh in a vessel of known weight, then heat in steam-oven till weight is constant. From the original weight and the loss of weight calculate the percentage of water.[1]

EXPERIMENT 40. To show that dried plant-material contains carbon and hydrogen. Burn some of the material obtained in Expt. 39. Hold a cold glass plate over the smoke from the burning plant, so as to condense any moisture formed. Hold a glass rod with a drop of lime-water at its end over the smoke, and note if the lime-water becomes turbid owing to the carbon dioxide given off.

EXPERIMENT 41. To obtain the percentages of combustible substances and of ash in the dry material of plants. Take some of the dry material obtained in Expt. 39, weigh and burn in a crucible of known weight. From the weights obtained, calculate the percentages. Preserve the unburnt material or ash for experiment 43.

EXPERIMENT 42. To show that nitrogen is present in plant structures. Crush some soaked peas in a mortar, place in a test-tube with soda-lime and heat. Test for ammonia fumes.

EXPERIMENT 43. To show the presence of certain elements in the ash of plants. Dissolve some of the ash in hydrochloric acid. Test the solution as follows: (*a*) On a platinum wire in the Bunsen burner, both with and without the cobalt glass. (*b*) With ammonium oxalate. (*c*) With potassium ferro-

[1] Loss of weight may be contributed to by other substances volatile at 100° C., but such loss is usually negligible.

cyanide. (*d*) With sodium hydrogen phosphate in presence of ammonium chloride and ammonium hydrate. The strong yellow coloration of the flame indicates the presence of sodium and possibly calcium ; when the cobalt glass is used, a violet coloration indicates the presence of potassium. A white precipitate with ammonium oxalate indicates the presence of calcium ; a blue colour with potassium ferrocyanide indicates iron and magnesium is indicated by a precipitate with sodium hydrogen phosphate.

Experiment 44. To show the presence of sulphur and phosphorus in plants. Heat some of the ash with a pellet of sodium, dissolve in water, and then test one portion with barium chloride and another portion with ammonium molybdate in nitric acid solution. A white precipitate with the first portion indicates sulphur, and a yellow precipitate with the second portion indicates the presence of phosphorus.

Experiment 45. To show that some plants contain acid substances. Pound some leaves of sorrel in a mortar, add a little water and filter. Test the filtrate with blue litmus paper. The leaves of rhubarb, *Oxalis*, sheep's-sorrel or some species of *Sedum* may also be used.

Water Culture.—Experiment 46. To show the methods of water culture. Prepare eight cylinders (see Expt. 9), of at least 700 c.c. capacity, fit them with corks, through which two holes have been bored. Place the plant in one hole of each cork, and a thistle funnel in the other, then pack the holes with cotton (sterilized in a steam oven) or with freshly ignited asbestos. Darken the cylinders by covering with paper which is black on one side, the blackened side being next to the glass.[1] Fill the cylinders with Sachs' solution which has been recently boiled and allowed to cool. Place the corks containing the plants in the cylinders. Put the water cultures on a shelf near a window, and replace the water absorbed by the plants with freshly-boiled distilled water. Do not let the solution get too warm or alkaline, correcting the alkalinity, if necessary, by adding a little phosphoric acid. A stream of air should occasionally be passed through the loosely-packed funnel, the plants should be brought into the open air sometimes, and the solution may have to be renewed. The seedlings should be as free from

[1] If the black side is outermost, heat will be absorbed, and the culture solution will become too warm.

germs as possible, being grown on sterilized material in a chamber with its air-holes plugged with sterilized asbestos. In the cylinders, the following solutions should be placed. (1) Sachs' solution. (2) Solution without any iron. (3) Solution without any potassium, sodium nitrate being added instead of the potassium nitrate. (4) Solution without any phosphorus, calcium nitrate replacing the calcium phosphate. (5) Solution without calcium, sodium sulphate and phosphate being used instead of the calcium salts. (6) Solution without any chlorine, the sodium chloride being left out. (7) Solution without magnesium, sodium sulphate replacing the magnesium sulphate. (8) Solution without nitrogen, another salt of potassium being added. In the solution without iron, development usually goes on fairly well, but the plant is yellowish instead of green so that we may conclude that chlorophyll cannot be formed when iron is absent from the solution. When nitrogen, or phosphorus, or potassium is absent the plant is feebly developed (Fig. 75). The plant is better developed when calcium or magnesium is absent, but is not so good as in the normal solution. The absence of chlorine does not appear to affect most plants.

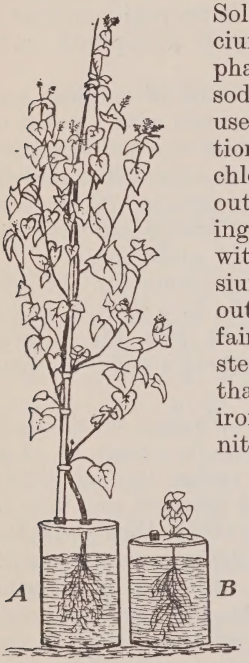

FIG. 75.— Water-culture of Buckwheat. After Nobbe, simplified.

A, normal solution. *B*, without potassium.

In the preceding experiments two methods have been adopted in order to find out what plants require. By the first method the substances actually present in the plant can be obtained, and we assume that such analyses give us a fair idea of the substances required by the plant; though some of the substances may not be actually needed, they may merely be incidental. By the second method of water culture the substances actually required by the plant are more accurately

shown. A large number of experiments performed on one plant would give us full information as to the materials requisite for the proper development of that particular plant.

Importance of Water-Supply. We have previously seen how important it is to have sufficient water in the plant, as it is the medium by which food and waste material are transported, is needed by the active protoplasm, and is necessary for growth and for maintaining the rigidity of the plant. The amount varies in different plants, in different parts of the same plant, and even in the same plant at different times. In leaves the percentage is usually over 80, whilst it is usually less than 5 in seeds. The percentage of water in such dormant parts of the plant as seeds is considerably less than in the active parts of the same plant, and before these dormant parts can resume activity they must be well supplied with water. We may consider the other substances present under two headings : (1) inorganic substances which are taken up by the root-hairs from the soil and are distributed in solution through the plant, and (2) organic substances present in the living material of the plant and as complex food or waste compounds.

Essential Inorganic Elements. The most important inorganic substances obtained in solution from the soil are compounds of potassium, calcium, magnesium, and iron in the form of nitrites, nitrates, sulphates and phosphates. By means of the chemical analysis of plants, by water culture and other experimental methods, potassium, calcium, magnesium, iron, nitrogen, sulphur, phosphorus, carbon, hydrogen, and oxygen have been shown to be necessary for normal life, but these are not the only elements present in plants, in fact, any soluble substance may be taken up in small quantity. Sodium is always present, but is unnecessary, since in a water culture solution without it a plant can develop normally. Manganese is also present, and it may be necessary to include this amongst the essential elements, as recent experiments indicate that complete development of the plant does not occur in its absence. Chlorine is often present, especially in plants growing near the sea, but it has been

shown to be non-essential except in a few cases (e.g. buckwheat). Silicon is often present, and in some cases (e.g. grasses and horse-tails) may be considered essential, as the plants do not attain their normal rigidity in its absence. Without potassium, nitrogen, phosphorus or sulphur, the plants are weak and ill-developed. Without magnesium or calcium, which probably act as bases for the neutralization of acid substances, the plants are smaller than when grown in a complete food solution. Without iron the plant lacks the green colour, chlorophyll being absent, though iron is not actually present in chlorophyll. In a maize plant, which has been grown in a culture solution devoid of iron, the green coloration can be produced on the leaves by brushing with a very dilute solution of ferric chloride.

Organic Substances. The organic substances are usually of a much more complex character, and have a much greater molecular weight than the inorganic salts. When these complex organic substances contain nitrogen they are known as proteids. Albumin, a proteid which is familiar to us as the substance forming the white of an egg, is found in many plants ; gluten is the proteid of the wheat grain, and is the sticky substance which causes flour to form a dough or paste ; legumin is the proteid found in peas and beans.

Organic substances which consist of carbon, hydrogen and oxygen, so that the proportion of the hydrogen and oxygen is the same as in water, are called **carbohydrates.** Familiar examples are starch $(C_6H_{10}O_5)_n$, cellulose $(C_6H_{10}O_5)_n$, grape-sugar $(C_6H_{12}O_6)$ and cane-sugar $(C_{12}H_{22}O_{11})$. When the non-nitrogenous organic substance consists of carbon and hydrogen only, it is a **hydrocarbon.** Many hydrocarbons such as turpentine $(C_{10}H_{16})$, olive and castor oils are obtained from plants.

CHAPTER XII

THE CELL AND ITS CONTENTS

All plants consist of little boxes or cells, which are arranged in various ways in different plants. Some plants are of a very simple nature, and merely consist of a single cell, whilst others are very complex and contain thousands of cells of different shapes, sizes, strengths and qualities. If we wish to examine an example of a simple plant, we can scrape off a little of the green scum (*Protococcus*, Fig. 191) which is so frequent on tree-trunks or walls, put it on a glass slip with a drop of water, place a thin circle of glass (cover-slip) on the top, and view it under a microscope. If we wish to examine the cells of a larger plant, we can scrape off a portion of the plant, and mount it in a similar way for microscopic examination. This method answers fairly well for the cells of some juicy fruits, such as the apple, elderberry and blackberry, but does not give satisfactory results if we wish to examine the cells of a root or stem. For these we are obliged to make sections, i.e. cut off slices thin enough to allow light to pass through them when they are mounted and placed under a microscope.

Cells of Onion. A fairly easy way of obtaining cells for microscopic examination is to take an onion, which, as we have seen, consists of a number of fleshy leaves on a short stem, and peel off the thin skin from these fleshy leaves. A little of this thin skin can easily be mounted in water or dilute glycerine (preferably the latter, as it does not dry up so quickly), and examined microscopically. It is seen to be formed of a large number of hexagonal or rectangular areas (Fig. 76), which at first appear to be empty, but closer examination reveals

the presence of something which has a greater refractive power than the glass on which the preparation is mounted, or the liquid which surrounds it. This substance is known as **protoplasm**, and is the basis of life. It is a colourless proteid, and cannot be seen, except in the same way that a colourless bubble of air can be seen in the glass of a window-

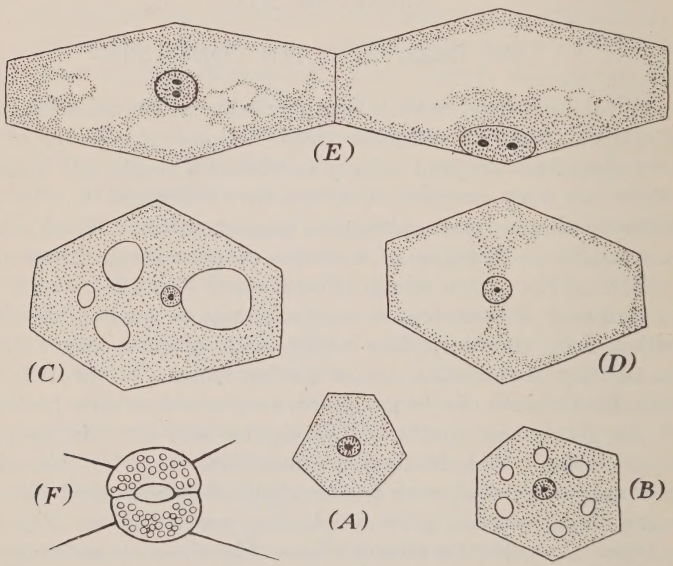

FIG. 76.—Cells from the Skin (Epidermis) of a juicy Scale-leaf of Onion Bulb.

A, young cell. *B*, *C*, *D*, *E*, older cells in progressive stages of development. *F*, stoma and guard-cells containing chloroplasts (obtained from the outer epidermis of the third fleshy scale-leaf of a bulb). All × 300. Protoplasm dotted, vacuoles left clear. In *B* and *C* the vacuoles are made more definite by lines round them, though such clear boundary lines cannot be seen in a microscopic view. Nuclei are enclosed by a line representing the nuclear membrane and nucleoli are darkened.

pane, i.e. by the refraction or bending that the rays of light undergo when passing through it. This protoplasm is the actual cell, and makes all the other substances which are found either within or around it. In plants, it usually manufactures **cellulose** from the food supplied to it, and forms a cell-wall of this substance around it. One portion of this protoplasm

seems to be thicker, and shows up as a rounded body. This body which is known as the **nucleus** is a very important part of the protoplasm, as it exercises a directive influence on the work done, and is specially concerned in the formation of new cells. In it, one or more denser portions are usually noticeable, especially if our preparations are irrigated with a solution of iodine, by placing a drop of iodine solution on one side of the cover-slip, and drawing it under the slip by means of a piece of blotting-paper at the other side. These dense portions are known as **nucleoli**, and may form a reserve of nuclear material when the cell is dividing. If the cells are taken from a young onion, we may find the protoplasm

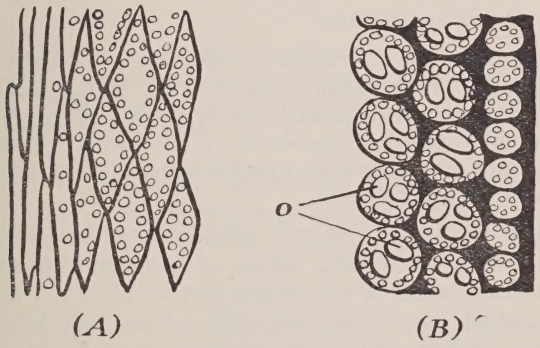

FIG. 77.—Chloroplasts.

A, cells of moss (*Bryum capillare*) leaf. The inner cells contain choroplasts, but these are absent from marginal cells. *B*, three rows of cells from the margin of a liverwort (*Odontoschisma sphagni*) leaf. The cells are thickened at the corners and all contain chloroplasts; oil bodies (*o*) are present in the inner cells (× 250).

filling all the space within the cell-wall, but in cells from an older onion the protoplasm forms a lining round the cell-wall, and there is a central space or **vacuole** containing cell-sap.

Chloroplasts. The skin of the onion scales is colourless, whereas many plant structures are of a green colour, and, if we wish to find out what the green colour is due to, we should examine the leaf of a moss (Fig. 77). It is better to obtain a moss with large cells, and such a moss is common on the soil of plant-pots in greenhouses. If a moss with

large cells is obtained from such a situation it is probably a moss called *Funaria*, though it may be a *Physcomitrium* or a *Bryum*, either of which will serve quite as well as Funaria. The leaf consists of a single layer of cells, except at the midrib, and each cell has a structure similar to that of the onion cell, but, in addition, there are such a large number of little green bodies (Fig. 77) present that the protoplasm lining and nucleus are not easily seen. The little green bodies or chloroplasts, which give the green colour to the leaf, consist of little bits of protoplasm with a green colouring matter (chlorophyll) diffused through it. They are able to absorb the light rays, and thus obtain the energy necessary for the synthesis of carbohydrate from carbon dioxide and water.

Experiment 47. To show the absorption of light rays by chlorophyll. Wash some green leaves, boil them for one minute in water, and warm them in alcohol till a green solution of chlorophyll is obtained. Examine by means of a spectroscope, and note that a part of the spectrum is absorbed, especially at the red end.

Starch Grains. The cells (Fig. 78) of the potato-tuber should also be examined. Slices or sections thin enough to be examined under a low power can be obtained by means of a scalpel. In these, the protoplasm has largely disappeared, and very little remains inside the cell-wall, except a large number of refractive grains, which may be shown to be starch grains by becoming blue when treated with iodine solution. These starch grains are formed by a small piece of protoplasm (**leucoplast**) which is able to change sugar into starch. The carbohydrate manufactured by the potato plant is passed down as sugar to the underground tubers, and the leucoplasts are then able to change this soluble sugar into insoluble starch, so that the process can continue. When the leucoplast encircles the starch, the latter is laid down in concentric layers, and the grains are small (e.g. wheat, Fig. 78, *D*), but when the starch is mostly deposited on one side (Fig. 79), the activity of the leucoplast is not interfered with so much, and these excentric grains (e.g. potato, Fig. 78, *A* and

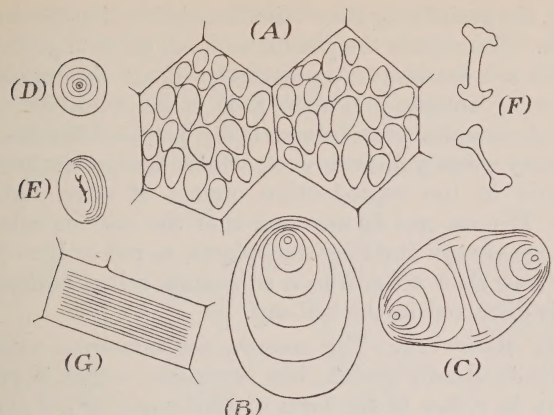

FIG. 78.—Starch-grains.

A, cells containing numerous starch-grains from the tuber of a potato (× 15). *B*, excentric starch-grain (× 150). *C*, compound starch-grain. *D*, concentric starch-grain of wheat (× 300). *E*, concentric starch-grain of bean (× 300). *F*, starch-grains from latex of spurge. *G*, raphides.

B), may be many times larger than the leucoplast which formed them. There is often a period of rest in the deposition of the starch, and, as one layer may contain less water than

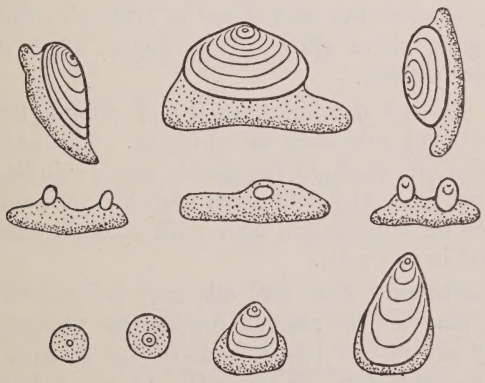

FIG. 79.—Formation of Starch-grains.

Leucoplasts (from pseudobulbs in the orchid *Phajus*) forming starch-grains (× 250). The four lower figures show the formation of starch-grains by the chloroplasts (× 250) in the parenchymatous cells of the stem of *Pellionia*.

another, the grains may show faint lines indicating the different deposits. Sometimes the plastid or small piece of protoplasm is neither a colourless leucoplast nor a green chloroplast, but is yellow or orange, and then it is called a **chromoplast.** Yellow chromoplasts can be seen in the petals of the dandelion or of many other yellow flowers, whilst orange chromoplasts are found in the reproductive organs of some flowerless plants. It must not be assumed that the various colours of flowers are always due to chromoplasts, as red or blue flowers usually owe their colours to a substance called anthocyanin which is dissolved in the cell-sap.

Sugar Reserves. The reserve carbonaceous substance in plants is usually starch, but sometimes sugar is present, and may be either in the form of cane-sugar ($C_{12}H_{22}O_{11}$) or grape-sugar ($C_6H_{12}O_6$). The former is present in the cells of the sugar-cane, beetroot, carrot, onion, etc., whilst the latter is often present in fruits. By treatment with Fehling's solution (potassium sodium tartrate, sodium hydroxide and copper sulphate solution) a reducing action occurs when grape-sugar is present in the cells of a plant, and a red precipitate of cuprous oxide is formed. When the sugar is cane-sugar, this reaction does not occur, but after boiling with a little mineral acid, the cane-sugar is broken down into two simpler sugars, one of which is grape-sugar, when the reduction can be effected.

Inulin. In the dandelion group of plants, the reserve carbohydrate is a substance called inulin. This has the same empirical formula ($C_6H_{10}O_5$) as starch, but is soluble in water, and does not give any coloration with iodine. On treating a thin slice of a dandelion root with alcohol, the inulin is precipitated in the cells.

Hydrocarbons. Fats and oils may be present in some cells, and may act as reserve substances, though, in some cases, they are merely by-products of the general chemical activity (**metabolism**) of the cell. In many foliose liverworts, special bits of protoplasm (**elaioplasts**) are concerned in the production of fatty matter, but it is very doubtful if the substances are reserves. The general statement may be

made that hydrocarbons in the higher plants are not reserves, whilst in the lower plants, especially in fungi, they are. The various aromatic oils produced in many of the flowering plants give them their characteristic odours.

Proteid Reserves. Nitrogenous organic substances are frequently produced in the cell, and act as reserves of nitrogen.

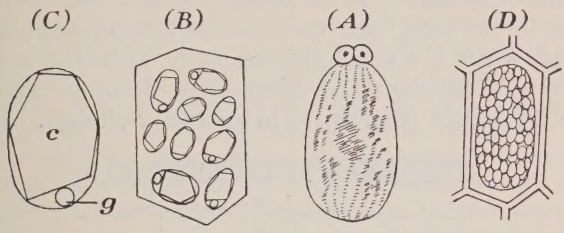

FIG. 80.—Proteid-grains.

A, seed of castor-oil plant (*Ricinus communis*). The presence of an aril and also the markings on the testa cause the seed to resemble a beetle. *B*, cell of endosperm with aleurone (grains × 350). *C*, single aleurone grain with crystalloid (*c*) and globoid (*g*) (× 1000). *D*, cell from seed of lupin with aleurone grains.

Such proteid or **aleurone** grains can be seen in the seeds of many plants ; e.g. maize (Fig. 10), lupin, castor-oil (Fig. 80), pea.

Crystals. Crystals of calcium oxalate (CaC_2O_4) and calcium carbonate ($CaCO_3$) are often found in the older cells of plants. In the cuckoo-pint (Fig. 87) the crystals of calcium oxalate occur as minute needles (**raphides**), and if a very small portion of the leaf is chewed and then placed at the tip of the tongue, a pricking sensation, which is commonly called the taste of the cuckoo-pint, is felt. It is probably owing to the presence of these raphides that the leaves of the cuckoo-pint owe their comparative immunity from the attacks of snails.

EXPERIMENT 48. To show that snails do not readily attack the leaves of the cuckoo-pint. Keep several snails without food for a couple of days. Place two in a covered vessel which contains fresh leaves of cuckoo-pint, and two others in a similar vessel containing other kinds of leaves (stock, wall-flower, etc.).

When the raphides are clustered together in more or less

spherical groups, they are called sphæroraphides. In some plants belonging to the nettle family, a space is formed just beneath the skin of the upper surface of the leaf, an ovoid framework of cellulose is formed in this space and on this framework crystals of calcium carbonate are deposited. The structure is known as a **cystolith** (Fig. 81).

Crystal-like bodies of a proteid nature are sometimes present in the cells, and these are called **crystalloids.** A **globoid,** which is a small globular body containing a double phosphate of calcium and magnesium, is often associated with a crystalloid (Fig. 80), as in the castor-oil seed. Resins,

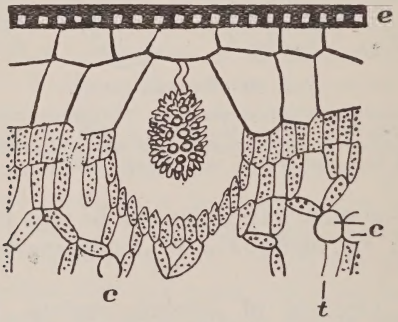

FIG. 81.—Cystolith.

Section of leaf of *Ficus elastica* showing a cystolith (× 200). *c*, laticiferous cells; *t*, cell containing tannin; *e*, thick-walled epidermis.

gums and mucilages are sometimes present in cells, whilst the sap of most plants contains organic acids or their salts.

Organic Acids. The acid taste of the lemon is due to citric acid, the grape contains tartaric acid, the apple malic acid and oak-galls tannic acid. The stinging hair of the nettle (Fig. 3, *A*) has a gland which manufactures formic acid at its base, whilst there is a little piece of silica on the tip. When the siliceous point is broken, the acid passes along the tube of the hair into the wound. Oxalic acid or its salts are present in some plants such as rhubarb, the leaf-stalks of which owe their taste to acid potassium oxalate. In the stinging nettle the formic acid acts as a protection against the

attacks of browsing animals, but in most cases the acids and acidic salts are due to incomplete oxidation. The osmotic activity of cells depends largely on the presence of such salts.

Osmotic Strength of Cell-sap.—Experiment 49. To determine approximately the osmotic strength of the cell-sap. (1) Take strips about 2 cm. long and 3 mm. wide of the inflorescence stalk of the dandelion, immerse in various strengths of salt solutions till one is obtained in which no further curvature occurs. (2) Strip off the outer layers of cells from a leaf, mount in varying strengths of salt solution and examine under the microscope, till one is found in which the cells beneath the epidermis remain almost unaltered after an immersion of ten minutes. If the solution has a higher osmotic pressure than the cell-sap, the protoplasm will lose water and contract away from the cell-wall (become plasmolysed). If the solution is too weak, no contraction will take place. When the solution is slightly stronger than the cell-sap, plasmolysis will begin to show and this solution may be taken as having an osmotic strength approximating to that of the cell-sap. The osmotic strength may be reckoned in atmospheres, by considering what ratio the strength of the equivalent solution bears to a gram-molecular one. A gram-molecular solution may be considered to have an approximate pressure of 22 atmospheres and our equivalent solution has a pressure in atmospheres of $22 \times \frac{\text{strength of equivalent solution}}{\text{strength of gram-molecular solution}}$. When a sugar solution is used, this result may be taken as approximately correct, but when dissociation occurs in the solution used, the pressure obtained will be greater, and a correction must be made. The amount of dissociation varies according to the salt used, the dilution, etc. An approximate correction is made by multiplying our result by $\frac{3}{2}$. For example, in a particular experiment, the strip of dandelion stalk did not show any further curvature in a 1·7 per cent. solution of potassium nitrate and the osmotic pressure is approximately $\frac{22 \times 17 \times 3}{101 \times 2} = 5{\cdot}6$ atmospheres. This approximate result is too small in this particular case, as dissociation in a 1·7 per cent. solution of potassium nitrate is greater than allowed for in the correction.

Cell Wall. The cell-wall is sometimes thickened or changed by substances stronger than, or different from, cellulose. Cells which become woody are said to be lignified, and this lignification is often stated to be due to the deposition of **lignin** on the cellulose framework. Cells which are lignified give a bright yellow colour with acid aniline sulphate and a red colour with phloroglucin and strong hydrochloric acid. It is convenient to term the matter which causes these reactions lignin, but it is improbable that it is a definite chemical substance. **Cutin**, which is often formed on the external parts of plants, is a substance possessing characters similar to the material composing our finger-nails. **Suberin** is formed in the cell-walls of the outer layers of woody plants, and is the substance to which cork owes its special characters.

The protoplasmic lining of the cell wall must have a considerable influence on osmosis. It appears to act as a semi-permeable membrane allowing dilute solutions to pass into the cell whilst the passage of salts in the opposite direction is prevented. The protoplasm in all cells is probably in continuous movement. This is not perceptible in most plants, but in some can be observed easily under the microscope. The cells near the midrib or the margin of an *Elodea* leaf show the rotation of protoplasm quite clearly, the chloroplasts being carried along like little boats by the stream of protoplasm. The staminal hairs of the spiderwort (*Tradescantia*) and the slender roots of the frog-bit (*Hydrocharis*) also show protoplasmic movement, that of the latter being a rapid one in comparison with that of *Elodea*.

CHAPTER XIII

POLLINATION

A few methods by which pollination is effected have been described in previous chapters. The pollen may be carried to the stigma by wind, water or animals. The animals concerned in the pollination of flowers are chiefly insects which, of course, come to the flower in search of honey, but in the golden-saxifrage, slugs crawling over the flower do the work of pollination, and in some American plants the

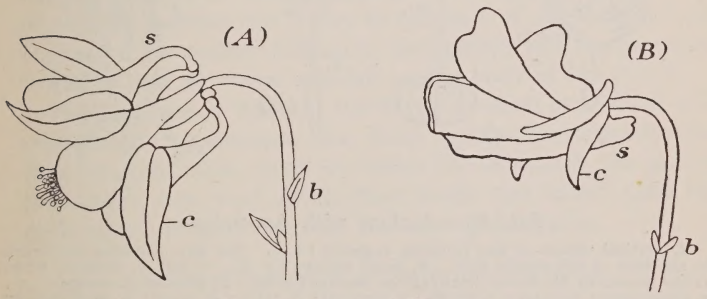

FIG. 82.—Spurred Flower.

A, columbine. *B*, violet. *s*, spur; *b*, bract; *c*, sepal of calyx.

work is done by humming-birds. Many flowers show little adaptation for a particular kind of insect; almost any kind of insect moving over the flower is able to carry the pollen. Such flowers as the buttercup, marsh-marigold, anemone, stitchwort, mustard and garlic may be said to be open for the visits of any flying insect; in fact such open flowers may sometimes be pollinated by means of wind or other agency. When we walk through a field of buttercups and disturb the

pollen with our boots, we may become the pollinating agents.

Protection against Honey-Thieves. These open flowers have little protection against honey-thieves, since creeping insects or other animals may crawl up the flower-stalk, and obtain the honey from below, without doing any service to the flower. In the wallflower, a certain amount of protection against burglars is afforded by two of the sepals becoming larger and so partly closing the entrance from below. In the violet (Fig. 82), larkspur and columbine (Fig. 82), one

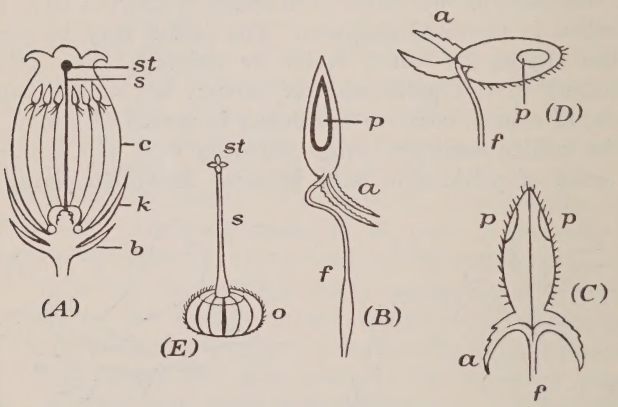

FIG. 83.—Anthers with Appendages.

A, vertical section of ling (*Calluna vulgaris*) (× 3). The two nectaries are shown at the base of the corolla tube. *B*, single stamen (× 15). *C* and *D*, different views of the stamen of fine-leaved heath (*Erica cinerea*) (× 15). *E*, pistil of *E. cinerea* (× 6). *a*, appendages; *b*, bract; *c*, corolla; *f*, filament; *k*, calyx; *o*, ovary; *p*, pore, through which the pollen is discharged; *s*, style; *st*, stigma.

or more of the petals may be spurred and enclose the nectary, so that a short-tongued insect cannot obtain the honey unless it bites through the spur. That burglary does take place is often shown in the violet, the spur having its tip perforated. In the campion (Fig. 132) and pea (Fig. 55) the sepals join together to form a calyx-tube which the thief must perforate in order to obtain the honey, and a still better method is adopted by flowers in which the petals have joined together to form a corolla-tube, e.g. heather, comfrey, primrose. In

some cases the corolla-tube has become so long (e.g. primrose, Fig. 85) that only insects with long " tongues " are able to obtain the honey at the base of the tube.

Discharge of Pollen. The manner in which the stamen splits to let the pollen escape is often correlated with the position of the nectary, and the method of entrance of the insect. In an open flower like the buttercup, the nectary forms a small bump near the base of the petal (Fig. 54, *D*) ; an insect obtaining the honey will have to pass part of its body on the outside of the stamens, and therefore the stamens should split on the outside if the pollen is to be deposited on the visitor. In a flower like the snapdragon, where the honey is at the base of the corolla-tube, the " tongue " of the insect will have to pass on the inside of the stamens, and therefore the pollen will be discharged from the inner surfaces of the anthers. In the strawberry-tree and many other members of the heath family, there are two projections at the back of each stamen (Fig. 83). These projections will be disturbed when the insect searches for honey at the base of the corolla-tube, tipping of the anther will occur and pollen will be discharged from the **apical pores** and fall on the body of the insect.

The presence of hairs in the flower is often connected with pollination ; sometimes the hairs are presentation-brushes (see the dandelion, page 83, where the stigma is the pollen-presenter), but very often they make the insect take the path which is most efficient for cross-pollination.

Contrivances for Cross-pollination

We have not yet considered the methods by which it is rendered more probable that pollen from another plant, rather than from the same one, is carried to the stigma. The simplest contrivance is to have two kinds of plants, one bearing stamens and the other carpels, and, though this is seldom shown in insect-pollinated plants, it is the method adopted by the red and white campions. Such plants are said to be dicœcious, i.e. they have two houses, one for the stamens and another for the carpels. Other familiar examples of dicœcious plants are willows (Fig. 140), dog's-mercury

(Fig. 59) and butcher's broom (Fig. 30). In some plants both stamens and carpels are present, but the flowers are not perfect, i.e. they do not contain both stamens and pistil, though the staminate and pistillate flowers are on the same plant, which is then said to be monœcious, e.g. hazel (Fig. 84), alder. In dicœcious plants, cross-pollination is the only kind which can occur, whilst in monœcious plants it is quite likely to occur, especially if the staminate and pistillate flowers are ripe at different times. In the cedar, which is monœcious, the staminate flowers are chiefly on the lower branches, whilst the pistillate ones are higher up, and therefore pollen is more likely to be blown from a neighbouring tree than from the same one.

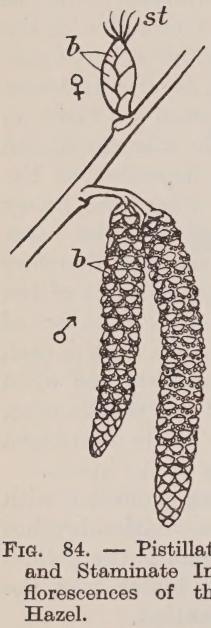

FIG. 84. — Pistillate and Staminate Inflorescences of the Hazel.

The pistillate (♀) inflorescence is somewhat exaggerated in size relatively to the staminate (♂) catkin. *st*, stigmas; *b*, bracts in whose axils the flowers are borne.

Dicœcious or monœcious plants are comparatively rare, but many plants are practically dicœcious or monœcious since the stamens and carpels in the same flower are ripe at different times. In insect-pollinated flowers, the anthers are usually ripe first (**protandrous**), but as this method involves a tremendous waste of pollen in wind-pollinated flowers, these have the stigmas mature before the anthers (**protogynous**). In some plants there are two lots of stamens, one lot being ripe before the pistil, whilst the second lot is ripe at the same time. In such plants, cross-pollination is the rule, but, if this does not occur, self-pollination can take place from the second lot of pollen.

INSECT POLLINATION

Some plants show special contrivances for cross-pollination, and a few of these will be noted below.

Primrose. In the primrose there are two kinds of plants. One kind has flowers (Fig. 85, *A*) which are often called "thrum-eyed," and in such flowers the five stamens are fixed on the top of the corolla-tube (when they are said to be epipetalous) whilst the single stigma is near the middle of the tube. The other kind of plant is said to bear "pin-eyed" flowers, because in each flower (Fig. 85, *B*) the pin-headed stigma is at the top of the corolla-tube, whilst the epipetalous stamens are fixed near the middle of the tube. An insect visiting a pin-eyed flower will get its "sucking-tube" dusted with pollen as it is thrust

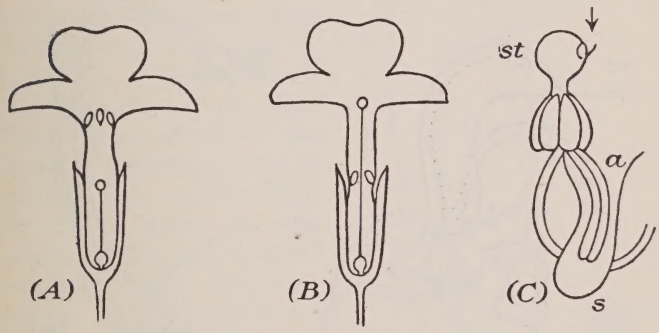

FIG. 85.—Heterostyly of Primrose.

A and *B*, vertical sections of flowers of the two kinds of primroses. *C*, flower of violet with all the sepals removed and only the spur (*s*) of the corolla remaining. Two of the stamens have appendages (*a*) which form nectaries, projecting into the spur of the corolla. *st*, stigma with receptive spot protected by a lid. The pedicel of the flower is shown and the way in which the insect approaches the flower is indicated by the arrow. Note that the natural position of the flower is more-or-less opposite to that shown in the figure.

down to reach the honey. If it visits another pin-eyed flower, the portion of the "sucking-tube" which is dusted with pollen will not come in contact with the stigma, but if it visits a thrum-eyed flower, the pollen will be deposited on the stigma. During this visit, the head of the insect becomes dusted with pollen from the stamens at the entrance of the corolla-tube, and when the insect visits a pin-eyed primrose the pollen will be deposited on the stigma. There is a possibility of self-pollination in the thrum-eyed primrose, but cross-pollination must occur in the pin-eyed plant.

Violet. In the violet (Fig. 82) one of the petals is modified to form a spur, into which two of the anthers send projections which function as nectaries. Above the stamens, the stigma (Fig. 85, *C*) forms a little round knob, but only a small portion is capable of receiving the pollen-grain. Below this receptive spot there is a little lid, fixed in such a way that an entering insect is able to deposit pollen on the spot, but when the insect is leaving the flower the lid is closed over the spot, so that pollen cannot be deposited. In this way self-pollination is prevented.

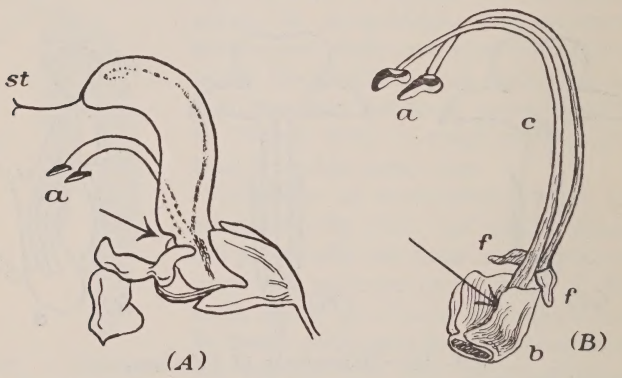

FIG. 86.—Sage (*Salvia*).

A, flower. The dotted line represents position of stamens before depression. *a*, fertile anther lobes; *b*, barren anther lobes; *c*, connective; *f*, anther-stalk (filament); *st*, stigmas. The arrow indicates where the insect enters. *B*, stamens removed from corolla.

Sage (*Salvia*). Most members of the dead-nettle family, to which the sage belongs, have four stamens which are ripe before the stigmas and take up a position in the flower which is occupied by the mature stigmas later on. The sage flower (Fig. 86) has only two stamens, each having two anther-lobes as usual, but only one of the anther-lobes is fertile, the other producing a little bump which is sterile, i.e. does not contain any pollen. The **connective** between the fertile and sterile lobes grows so that the two lobes become widely separated, and a kind of lever is formed. The fertile anther-lobe occupies

the position usually taken by an anther in a flower of the dead-nettle family, whilst the other end of the lever is formed by the sterile anther-lobe (Fig. 86, *b*). An insect, searching for honey, disturbs the sterile part of the lever, and tips up the other, so that pollen falls on its body. When it visits an older flower the stigma is in the right position to receive the pollen.

Cuckoo - pint (*Arum*). The greenhouse plant which we call the arum lily is really not a flower at all, but consists of a white bract which sheathes the flowers. The hedges of many country-sides contain similar plants, which are wild arums, but are usually called cuckoo-pints or lords-and-ladies. The flowers (Fig. 87) are on a fleshy axis which sticks up like a poker inside a green sheathing bract. The sheath is constricted at one part, and the real flowers are below this constriction. The flowers are very simple ones without any sepals or petals, and are fastened on the lower part of the "poker." The pistillate flowers are at the base whilst the staminate flowers form a ring just below the constriction. In the constriction itself some flowers occur, but they have become barren. They look like flowers with long hairs at the

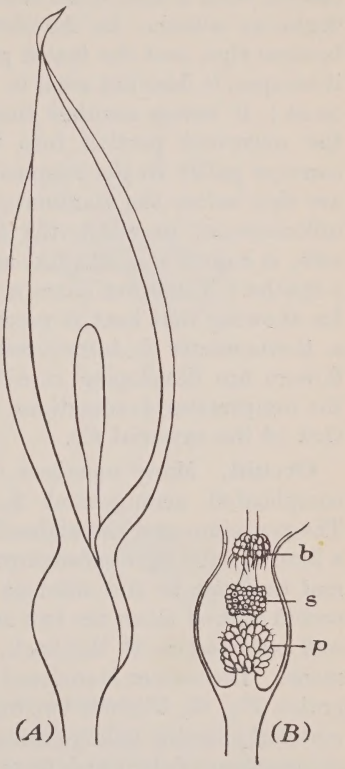

FIG. 87.—Cuckoo-pint.

A, inflorescence (spadix) in bract (spathe). *B*, lower portion of spathe opened to show flowers. *b*, barren flowers, with hairs closing up the constriction so as to prevent insects from escaping; *s*, staminate flowers; *p*, pistillate flowers.

top, and may be regarded as rudimentary flowers. The hairs are so arranged that a small insect can easily pass down into the small chamber below the constriction, but cannot return, and must remain a prisoner until the hairs begin to wither. In the meantime, the staminate flowers become ripe, and the insect gets dusted with pollen. When it escapes, it does not seem to be averse to a second imprisonment; it enters another sheath, passes along the hairs in the narrowed portion into the lower chamber and thus conveys pollen to the stigmas of the pistillate flowers, which are ripe before the staminate ones. This particular kind of inflorescence, in which the flowers are sessile on a fleshy axis, is known as a **spadix**, and the enclosing bract is called a spathe. The lower chamber of the wild arum is also useful for showing that heat is produced during active growth. If a thermometer is introduced into the chamber when the flowers are developing rapidly, about the middle of April, the temperature is sometimes shown to be two degrees above that of the external air.

Orchid. Many members of the orchid family exhibit a complicated arrangement for cross-pollination (Fig. 88). The gynecium and the andrecium grow up together and form a kind of tube (**gynostemium**) with the ovary at the bottom and the stigmas and stamens at the top. In the particular orchid figured there are two stigmas at the sides of the tube and one stamen at the back, and this is the usual arrangement. The stamen is enclosed in a little pouch, and the pollen-grains (Fig. 88, *D*) are in two bunches (**pollinia**). Some sticky material joins the pollen-grains together, and this sticky material continues downwards so as to form a stalk which expands at the base into a little disc. An insect entering the flower disturbs the pouch whilst it is drilling for honey[1] and the sticky little discs become attached to the head of the insect. At first they stand almost erect, and if the insect visits another flower immediately, they will not come into contact with the stigmas at all, but only with the rim of the tube above the stigmas. The stigmas are just inside the rim, and therefore the pollinia

[1] There are no nectaries in the orchid.

ought to lie flat on the top of the insect's head if pollination is to be effected. We find that this occurs and that it occurs in the right way (Fig. 88, *C*), the bending being towards the tip of the head, so that the pollen is able to touch the stigmas. The action of a bee in carrying pollinia can be easily imitated

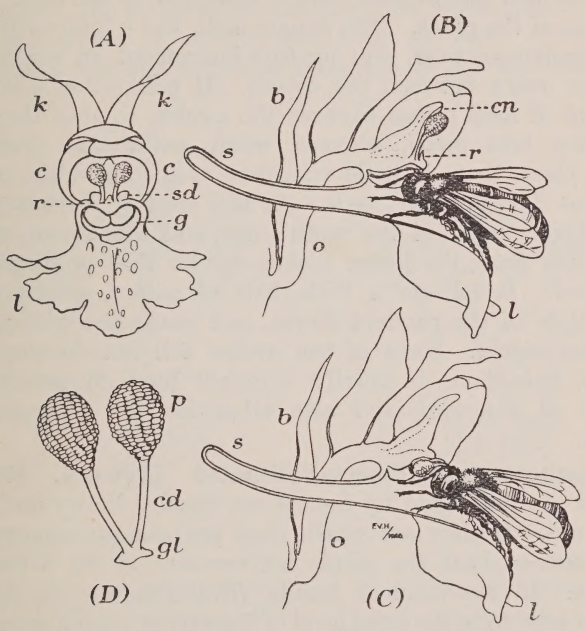

FIG. 88.—Orchid and its Pollination.

A, front view of flower. *B*, vertical section of flower showing the bee in the act of removing the pollinia. *C*, V.S. showing the bee bringing foreign pollinia which are in contact with the stigmatic surfaces of the gynostemium. *D*, pollinia of a single stamen. For the sake of clearness, the parts of the flower are outlined only, whilst the bee is shaded. *b*, bract; *c*, inner segment of perianth; *cd*, candicle; *cn*, connective; *g*, gynostemium; *gl*, glandula or viscid disc; *l*, labellum or lip; *k*, outer perianth-segment; *o*, ovary; *p*, pollinium; *r*, beak of rostellum; *s*, spur; *sd*, staminode or barren stamen.

by passing the sharp end of a pencil into the flower. On withdrawing it, the pollinia stand erect, but gradually bend over towards the point of the pencil, which can then be easily introduced into another flower so that the pollen comes into contact with the stigmas.

Yucca. In the examples given above, the pollen does not appear to be carried intentionally by the insect; the carriage of the pollen is a mere incident of the insect's search for food. In the Yucca pollination seems to be intentionally performed by the insect. The pollinating insect is a special moth (*Pronuba*) which flies at dusk, and is attracted by the large white flowers of the plant. The female moth has a long ovipositor or egg-placing tube, and by this instrument an egg is laid in the ovary between the ovules. If pollination occurs, a stream of food passes towards the ovules, so that they can develop into seeds, whereas, when pollination does not take place, there is little transport of food and the ovules do not develop into seeds. As this food is necessary for the development of the moth's egg, and the growth of the resulting grub, the insect makes certain that pollination is effected. It collects a little ball of pollen, climbs down the style of the pendent flower, and packs the pollen ball on the stigma. Some of the ovules will not develop into seeds, but there is usually sufficient food to satisfy the needs of the grub and also allow for the formation of seeds.

Characters of Insect-Pollinated Flowers. Flowers which are pollinated by insects are usually showy and conspicuous. If they are small, they are usually arranged in bunches, so that the whole inflorescence is the attractive object. In the hemlock family (Umbelliferæ), the flower-stalks arise from the same level of the axis of the inflorescence, and in such an **umbel** (Figs. 89, 126), as it is termed, many small flowers are near to each other. A similar device is adopted by the mustard family (Cruciferæ). The pedicels do not originate at the same level, but the top flowers have shorter stalks than the lower ones, so that the flowers are crowded together. An inflorescence of this kind is termed a **corymb** (Fig. 90). The aggregation of flowers is still more pronounced in the dandelion family (Compositæ), where they form a capitulum or head, which is usually spoken of by the uninitiated as a flower. In some plants, e.g. guelder rose and some members of the Compositæ, the outer

flowers are barren, and are merely devices for attracting insects to the inner fertile flowers.

The flowers usually have nectaries producing a sugary liquid (nectar) which attracts insects. They are often odorous, the scent being an indication to the insect that food can be obtained. The stamens are usually ripe before the stigmas and the pollen is usually sticky or gummy. Protandry involves a wastage of pollen from the first-formed flowers,

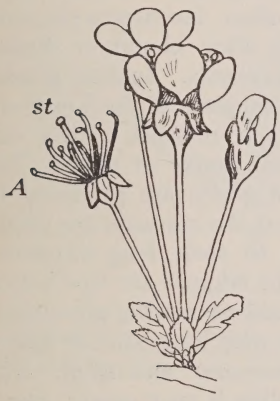

FIG. 89.—Simple Umbel of Cherry.

It is represented in a vertical position though naturally the flowers are drooping. *A*, andrecium of flower from which the petals have fallen off; *st*, stigma.

FIG. 90.—Diagrammatic Representation of Corymb.

b, bract with flower in its axil; *s*, stipule of ovate leaf.

but the wastage is less than if the ovules of the same number of flowers had been wasted.

The stigmas are sticky, and are usually less prominent than in wind-pollinated flowers. Owing to the less prominent positions occupied by both the stigmas and the stamens, greater protection is afforded. Hairs or other devices are often present, either to act as pollen-presenters, or to limit the movements of the insects so as to make them take the paths most efficient for pollination.

Wind-pollination

This is a common method which is exhibited by the members of the nettle, goosefoot, oak, sedge, grass and pine families, as well as by some species of families in which most species are insect-pollinated. In the rose family (Rosaceæ) most flowers are insect-pollinated, but the salad burnet is pollinated by means of wind. In the dock family the persicarias are insect-pollinated, whilst the docks are wind-pollinated.

Chief Characters of Wind-pollinated Plants. The flowers are often inconspicuous, and the petals are often absent or similar in colour to the sepals. In some plants, the non-essential parts of the flower are absent or much reduced. They are usually without honey or scent. The smooth pollen grains are produced in abundance, and the stamens are prominent owing to their long filaments (Fig. 91). The stigmas are ripe before the stamens, and are usually prominent, and provided with long hairs in which the pollen becomes entangled. The wastage of pollen is very great; much of it never reaches the stigma at all, but is scattered on surrounding objects. In many plants, especially trees, the flowers appear before the leaves which might prevent the pollen from reaching its proper destination.

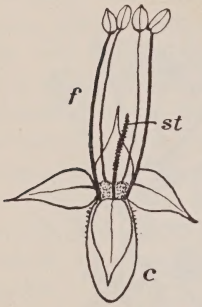

Fig. 91.—Wind pollination.

Flower of ribwort plantain (*Plantago lanceolata*) with bracts and calyx removed. The stigma is ripe before the stamens elongate and shed their pollen. *c*, corolla tube; *f*, long filament of stamen; *st*, stigma.

Explosive Stamens. In some plants, as the stinging nettle and the pellitory-of-the-wall, the stamens explode when conditions are suitable for pollination, and this device is of some use in preventing excessive waste. This puffing of the stamens may be seen if one watches the flowers of a staminate nettle (the nettle is diœcious) on a dry day. The process may be accelerated by pushing the point of a pin to the base of a ripe stamen, when the stamen flies up and a little cloud of pollen is shot out.

Water-pollination

In most aquatic plants, the flowers are raised above the level of the water and pollination is effected by either insects or wind. Even in these the pollen may sometimes be carried by water, but when the flowers are submerged, as in some of the pondweeds, the carriage of the pollen must be effected by water. Some interesting devices are resorted to by some of the pondweeds, and one of these methods is well shown in a foreign plant known as *Vallisneria*. The pistillate flower

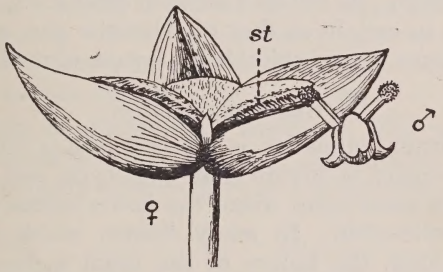

Fig. 92.—Water-pollination of *Vallisneria* (×10).

The pistillate flower at the surface of the water is attached to the substratum by a long stalk and its stigmas (*st*) are recurved. The stamens from a free-floating staminate flower (broken away from submerged staminate inflorescence) rub against the stigmas.

is carried by means of a long stalk to the surface of the water, and its large stigmas curve downwards towards the water. The staminate flowers are small and numerous, break off below the surface of the water, float to the surface and one of its two stamens rubs against the stigma of the pistillate flower.

Advantages of Cross-pollination

When cross-pollination occurs better seeds are produced than when the pollen comes from the stamens of the same plant. The seeds are better because they are able, on the whole, to produce plants which are more vigorous in withstanding competition and have greater ability in adapting themselves to their environments. A flower is then most fully organized when at its highest efficiency for cross-

pollination and when exercising the greatest economy in other respects to ensure the continuance of the race. Besides its efficiency and economy in pollination, its methods for protecting the seed during development, and for dispersing it later on must be taken into account. The reproductive apparatus of a plant may be highly organized in some respects but not in others, as, for example, in the orchids. Most orchids are highly developed in regard to cross-pollination; the seed is well protected during its development, and is so light that it is readily dispersed: but that lightness may prove a disadvantage. As the seed contains little food, its germination is not so certain as that of a heavier one, containing a greater amount of food suitable for the use of the infant plant.

Self-pollination

Though cross-pollination is the best, self-pollination often occurs, especially in flowers of an open type, and may be the rule even in some cases where the flower seems constructed for cross-pollination. In many flowers which are usually cross-pollinated, the failure of the usual method does not mean the failure of seed. Devices for self-pollination may occur, and one of these has already been described for the dandelion.

Some plants flower early in the year and, if weather conditions are unsuitable, the seeds may not develop properly. In many of these plants provision is made for the continuance of the species by vegetative means; e.g. the lesser celandine has tuberous roots (Fig. 31); in others, peculiar flowers are produced later on in the year. These flowers can be found during July on the violet and wood-sorrel, though they require searching for, as they remain green and bud-like. Since these flowers remain closed-up and are self-pollinated, they are termed **cleistogamous.**

CHAPTER XIV

FERTILIZATION AND SEED-FORMATION

Pollination is merely a preliminary to other changes which result in what is called fertilization, a process in which a cell from the pollen joins with a cell in the ovule, these two cells being termed germ-cells or **gametes.**

Formation of Generative Nucleus. The pollen-grain varies in size and shape according to the particular species of plant, but in many cases is more or less spherical and about

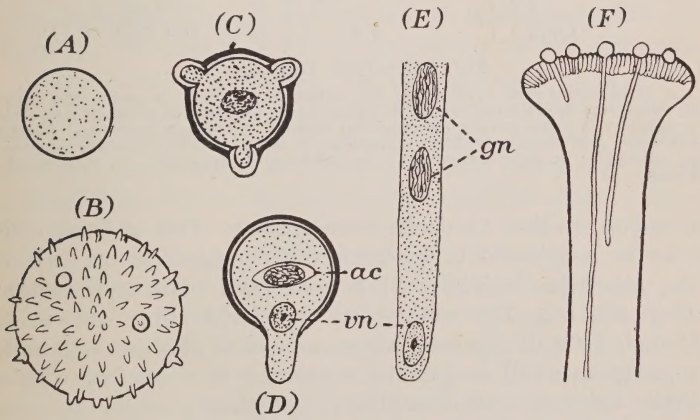

FIG. 93.—Pollen-grains.

A, of buttercup. *B*, of gourd showing embossed lids of the exosporium, which are pushed off when the endosporium protrudes to form pollen-tubes. *C*, of enchanter's nightshade; sectional view showing exosporium with three thinner areas. *D*, germinating pollen-grain showing antheridial cell (*ac*) and vegetative nucleus (*vn*). *E*, lower end of pollen-tube with vegetative nucleus (*vn*) and two generative nuclei (*gn*). All × about 250. *F*, stigma and style showing germinating pollen-grains (× ca. 13), diagrammatic. The receptive clavate papillæ of the stigma are indicated but other cells are not shown.

40μ in diameter.[1] It has two coats, a delicate inner covering (*endosporium*), and an outer and stronger skin (*exosporium*), in which thinner areas are present. When the pollen-grain reaches the stigma, it begins to grow, the exosporium is ruptured at one of the thinner areas, the endosporium protrudes and forms a slender filament which is called the *pollen-tube*. This penetrates the tissues of the style, and grows down to the ovary, feeding on the sugar or other food present in the cells of the style. Before the formation of this pollen-tube, the nucleus of the pollen-grain had divided

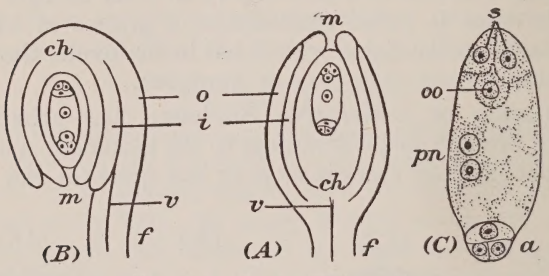

FIG. 94.—Ovule (Enlarged).

A, orthotropous ovule (*Polygonum*) just before fertilization. *B*, anatropous ovule. *C*, embryo-sac before fertilization. The polar nuclei (*pn*) have approached each other preparatory to fusion to form the vegetative nucleus. Protoplasm dotted and vacuoles left clear. *f*, ovule-stalk (funicle); *ch*, chalaza; *a*, antipodal cells; *i*, inner integument; *m*, micropyle; *o*, outer integument; *oo*, oosphere; *s*, synergidæ; *v*, fibro-vascular bundle.

into two, so that two cells were present. One of these cells may be considered to be the ordinary *vegetative cell*, whilst the other (*antheridial cell*) is concerned with reproduction (Fig. 93, *D*). The antheridial cell divides into two cells, though no wall separates them, and each of these is a male reproductive cell or gamete, consisting of a nucleus with a little ordinary cell-protoplasm (*cytoplasm*) round it. On reaching the ovule, the pollen tube enters through the micropyle, and one of the male gametes fuses with a female gamete, the formation of which will be described below.

Formation of Oosphere. The ovule is a stalked body,

[1] μ = micromillimetre = 0·001 mm.

consisting of a central mass of cells (*nucellus*) with one or two coats (*integuments*) enclosing it except at the micropyle (Fig. 94). One particular cell near the micropylar end of the nucellus enlarges to such an extent that it often fills up the ovule, using up and displacing the nucellar tissue. Then the nucleus of this cell, which is the *embryo-sac* or *megaspore* (Fig. 94, *C*), divides three times in succession, so that eight nuclei are present. These arrange themselves so that there are three at each end, whilst the remaining two join together in the middle to form a vegetative nucleus. The three near the micropylar end form the *egg-apparatus*, and are arranged in the corners of an imaginary triangle with its base towards the micropyle. The inner cell is the one which eventually fuses with the male gamete, and so must be the female gamete (Fig. 94, *oo*) or egg-cell (*oosphere*). The two other cells are placed between the micropyle and the important egg-cell and, as the pollen tube passes between them, apparently serve as guides for the proper passage. The three cells at the opposite end of the embryo-sac are called *antipodal cells*, take no further part in the process, and gradually disappear.

Formation of Embryo. The body produced by the fusion between the female gamete (*egg-cell*) and the male gamete (*generative nucleus*) is called the *egg* or *zygote*, and this, together with the parts around it, proceeds to form the seed. Before the egg begins to divide, the vegetative nucleus of the embryo-sac divides by *free-cell formation*, i.e. a large number of nuclei are formed and then cell-walls are laid down between them. The tissue thus produced is called the endosperm and is a storehouse of food for the developing egg. Division of the egg occurs in several ways, but, no matter what method is adopted, an embryo consisting of a radicle, two cotyledons and a plumule is formed (Figs. 7 and 8) when the seed is that of a Dicotyledon. In a Monocotyledon, only one cotyledon develops (Figs. 10 and 11), whilst in the group of plants (Gymnosperms) to which the pine belongs, besides other differences, there may be more than two cotyledons. The stalk of the ovule becomes the seed-stalk, and the integument (or integuments) becomes the seed-coat.

In the seeds of the bean, mustard, and many other plants, the **endosperm** is all used up, but in such seeds as those of the spindle tree and grasses, some of it remains (Figs. 10 and 11), and is used as a food reserve when the seed germinates. In some cases, e.g. pepper and banana, some of the nucellar tissue is not used up during the growth of the embryo-sac. This tissue persisting between the seed-coat and the embryo is known as **perisperm.**

Any extra growth on the outside of the seed-coat is termed an **aril.** In the yew it is a red juicy cup, in the willow-herb it is hairy (Fig. 70) and in the castor-oil it forms the head of the beetle-like seed (Fig. 80, *A*). Other familiar examples of aril are the orange-coloured investment of the spindle tree and the net-like mace of the nutmeg.

Meaning of Fertilization. The egg is produced by the union of two germ-cells. The smaller and more active of these is called the male gamete whilst the larger and more passive one is known as the female gamete. If the two gametes have come from different plants, the egg may have more potentialities than if they had come from the same plant. In the former case there is a greater possibility of a plant possessing such a combination of characters as to make it a vigorous one (see p. 127). If both the germ-cells have come from the same plant their potentialities are presumably the same, unless the plant is of hybrid origin (see Chap. XXV), and there seems to be little advantage in fertilization except that the amount of material is augmented or some necessary stimulus set up. It may also be considered that as the habit of fertilization is useful when the germ-cells come from different plants, the habit persists even when the two gametes come from the same individual. Reproduction by means of an egg which is the resultant of fusion between two germ-cells, is said to be sexual. In some plants the unfertilized egg-cell may develop into an egg, and then parthenogenesis is said to occur.

CHAPTER XV

MICROSCOPIC STRUCTURE OF THE STEM

When the stem arises from the division of the cells during the growth of the egg, it will, at first, consist of few cells, and each cell will have little difficulty in obtaining food and getting rid of waste material. For these processes osmosis between the cells is sufficient, but as the stem becomes larger, difficulties will arise.

Need for Differentiation. The outer layer of cells will be more exposed than the inner, and in some way or other, these outer or epidermal cells must be differentiated so as to form a protective covering. Then the internal cells will soon experience difficulties in regard to the transport of water and substances dissolved in it, and some differentiation for these purposes must occur. At first, a mere lengthening of the cells may suffice, but when the stem gets longer still, it will be much better for some cells to arrange themselves in longitudinal rows, and form continuous tubes through which the solutions can be conveyed. Then again, with the increase of length, it will be useful if some cells form strengthening material which may act as girders. The amount of differentiation exhibited by a stem varies to a great extent ; e.g. a stem of a plant which grows in shady places will not require such a strong epidermis as the stem of a sun-plant, and a creeping stem will require weaker girders or less supporting tissue than an erect one, other things being equal. The disposition of the water-conducting tissue, or of the strengthening tissue, may also vary, e.g. the girders in a cylindrical stem may be arranged differently from those in a rectangular one (Fig. 99). In certain groups of plants the disposition of the tissues is

also different; the arrangement of the strengthening and water-conducting tissue (**fibro-vascular tissue**) is on a different plan in a fern than it is in a flowering plant and, even in the latter, the plan is different in Monocotyledons from that in Dicotyledons (cf. Figs. 95 and 105).

In order to obtain a knowledge of the disposition of the cells, we must make sections of the stem, not only across it,

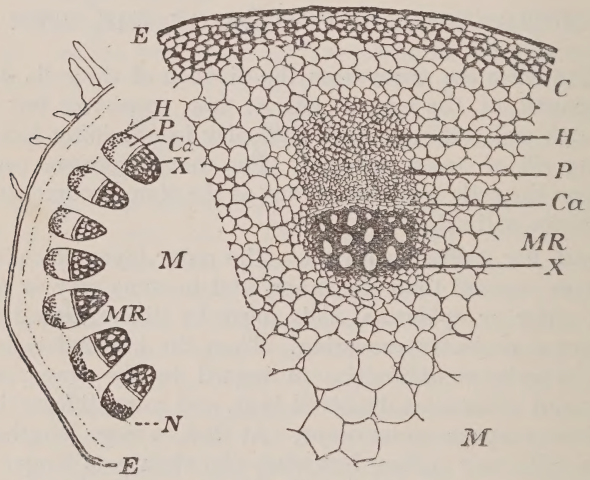

FIG. 95.—Stem of Dicotyledon.

Portion of T.S. of artichoke stem and sector more highly magnified (× 70). *C*, cortex with outer cells thickened; *Ca*, cambium; *E*, epidermis with hairs and thickened cuticle; *H*, hard bast (thickened pericycle); *M*, pith (medulla); *MR*, Medullary ray; *P*, phloem; *X*, wood (xylem); *N*, Endodermis.

but also along its length, and examine such sections under the microscope. At the growing-point, the cells are in an active state of division, and such an actively-dividing tissue is known as a **meristem**. When the cells are thin-walled and about as long as broad, the tissue is termed **parenchyma**. The use of the term parenchyma is not a very strict one, as the term is often applied to a tissue in which the cells are at least twice as long as broad. When the cells are much longer than broad, the tissue is termed **prosenchyma**.

Young Stem of Dicotyledon

A fairly typical example of the stem of a Dicotyledon is that of the artichoke. Sections of a very young stem, just below the growing-point, show a very slight differentiation of the cells into three groups. The outer layer eventually gives rise to the protective skin or epidermis, the central cells form the stele in which the conducting tissues are developed, whilst the intermediate layers form what is known as the cortex. We can study these in sections of a little older portion of the stem.

Epidermis. The epidermis consists of one layer of more or less rectangular cells, which are protective to those further in, and are therefore differentiated for this purpose (Fig. 95, *E*). The outer peripheral walls are thickened with a substance (cutin) which is stronger than cellulose and more resistant to the loss of water. Each of the cells deposits cutin on its outer wall, so that there is a continuous skin of this substance enveloping the outside of the stem. This *cuticle*, as it is called, is therefore not a layer of cells, but merely the conjoint product of all the epidermal cells. As the epidermal cells are chiefly of a protective nature, it is not necessary for the mature cells to contain much protoplasm, indeed, it is better for the organism to have its outer layer of cells dead, or almost so, as they are then less susceptible to injurious substances. Our own bodies are covered by an epidermis of dead cells, and consequently we are able to handle poisons and other injurious substances. In a full-grown plant, we may then expect the epidermal cells, whose work is the passive one of protection, to contain little or no protoplasm, but if some of these cells have active work to do, the living protoplasm will be retained. Such active cells are necessary around the pores (*stomata*) through which transpiration takes place, and will be more particularly considered in the chapter dealing with the microscopic structure of the leaf (see Chap. XVII). In most stems some of the epidermal cells grow out to form hairs, whilst in some plants, glands, prickles or other emergences are produced.

Cortex. The cortical cells (Fig. 95, *C*) may be roughly divided into three parts, an outer layer or *hypodermis*, intermediate layers or *mesodermis*, and an inner layer or *endodermis*. The hypodermis in the artichoke, and many similar plants, consists of elongated living cells with walls thickened at the angles, and this *collenchyma* (Fig. 98, *E*), as it is termed, serves as an extra protection and also increases the rigidity of the stem. The mesodermis consists of thin-walled cells lined with protoplasm containing chloroplasts, and can therefore form some of the starch required by the plant. In order to allow for the aeration of the stem, the walls of these cells do not fit closely against each other, small intercellular spaces being left through which gases can pass. Resin-canals are sometimes present, especially in an older stem. An intercellular space is lined by thin-walled cells (*epithelium*), which secrete the resin into the space, and usually the cells forming the layer around the epithelial cells are somewhat thickened (Fig. 168, *B*). The endodermis forms a boundary between the mesodermis and the stele, and consists of more or less rectangular cells containing abundant small starch grains, so that the endodermis shows out as a blue line on suitably staining with iodine and viewing under a low power of the microscope.

Stele. The cells of this may again be put into three groups : (*a*) an outer group, termed the *pericycle*, (*b*) a central core of cells forming the pith or *medulla*, and (*c*) an intermediate ring containing the fibro-vascular bundles and the tissue (*medullary rays*) between them. The cells of the pericyle are very variable in different dicotyledons. In the artichoke (Fig. 95, *H*), they are thin-walled outside the medullary rays but thick-walled outside the fibro-vascular bundles, so that each bundle appears to have a cap on its outer portion. These caps were formerly included with the bundles under the name of hard bast. The cells are elongated (Fig. 97, *Pe*), are thickened evenly all the way round, and are lignified, so that they serve as extra girders for maintaining the rigidity of the stem. Groups of thickened cells like these are termed *sclerenchyma* (Fig. 100, *HB*).

Phloem. The fibro-vascular bundles (Fig. 96) are very important structures in the stem, since, as their name implies, they form the fibres, or strengthening tissue, and also the vascular tissue through which water and the contained nutritive or waste material is conducted. The outer portion of each bundle is called the phloem, or bast, and is composed of three different kinds of cells. The most important are

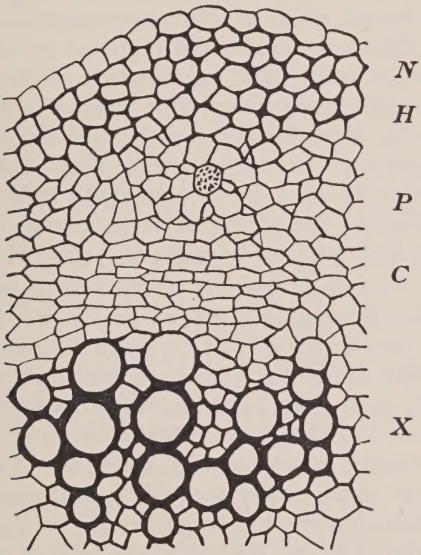

FIG. 96.—T.S. of Artichoke Stem (*Helianthus tuberosus*).

C, cambium; *H*, pericycle (little thickened as the stem is young); *N*, endodermis *P*, phloem (sieve-tubes and companion-cells, one sieve-plate shown); *X*, xylem. (× 200.)

those which are arranged end to end to form long rows of cells, and known as *sieve-tubes*, because the end walls (*sieve-plates*) are perforated. They function in the translocation of organic material, though the method of translocation is not understood thoroughly. Each sieve tube must develop from ordinary parenchyma cells of the young stem. A longitudinal row of such cells, as the stem gets bigger, so develops that the greater increase in size is lengthways, and then the end

walls become perforated to form the sieve plates. Each cell of the primary longitudinal row divides lengthways, so that two longitudinal rows are actually formed. One of these eventually becomes the sieve tube (Fig. 98, *C* and *D*), whilst the cells of the other remain much narrower and do not have their end-walls perforated. The latter are known as *companion cells*, and may be useful as temporary storehouses when the sieve tubes are blocked with organic material. The third lot of cells, phloem parenchyma, are ordinary cells which fill up the spaces not occupied by the sieve tubes and companion cells. For examination of the phloem, the stem of the cucumber (or vegetable marrow or white bryony) is useful as the sieve-tubes are wider and shorter than those of the artichoke. In consequence, sieve-plates are much more likely to be seen in section made from these stems. In some respects the stems of these plants are abnormal (see p. 182), and must not be taken as typical of Dicotyledons.

Xylem. The inner portion of the bundle consists of the xylem, which is commonly known as the wood, since many of its cells are lignified, and give the characteristic colour reaction with aniline sulphate or with phloroglucin and hydrochloric acid. The most important parts are the vessels (Figs. 96 and 97) along which the very dilute solutions are conveyed, chiefly in an upward direction. The passage of water is very much easier through a continuous tube than through a tube interrupted by end walls, so that, during the growth of the stem, we find that the cells in a longitudinal row enlarge, especially lengthways, and then the end-walls become almost entirely absorbed. As the stem gets bigger, more water will have to pass through it, and therefore the vessels (*tracheae*) must not only be wider, but also made of stronger material. In the supply of water to a growing human community, the original water pipes which sufficed for a hamlet will not be adequate for a town, and often have to be replaced by larger and stronger pipes. In a growing plant, the relaying of the pipes does not appear to be feasible. There is a possibility for very young pipes to get larger, but, when the walls are thickened, any enlargement will be very

slight. In our growing stem, the only possible way to provide a larger vascular system seems to be an increase in the number of pipes, and for the later formed pipes to be wider. The walls of these pipes or vessels must also be stronger, not only because wider pipes require stronger walls, but also because they help in maintaining the rigidity of the stem.

Annular, Spiral and Pitted Vessels. We find that the walls are thickened in various ways. In the first vessels (*protoxylem*) formed, and therefore in those which were present

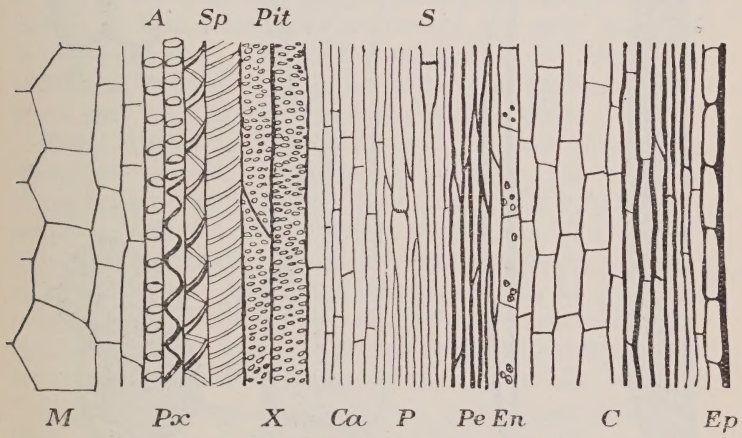

FIG. 97.—Radial L.S. of Young Artichoke Stem.

A, annular vessel; *C*, cortex; *Ca*, cambium; *En*, endodermis with starch grains; *Ep*, epidermis; *M*, medulla; *P*, phloem; *Pe*, pericycle; *Pit*, pitted vessel; *Px*, protoxylem; *S*, sieve-tube; *Sp*, spiral vessel. Diagrammatic, × about 130.

in the stem when it was much smaller, the cellulose walls are strengthened by rings of lignin (Fig. 97, *A*), or by a spiral (Fig. 97, *Sp*) of lignin, just as a paper tube can be strengthened by gumming hoops or a spiral of tinfoil on the inside. In the stem which is a little older and bigger, the spiral may be more closely wound round, and there may be two (or more) spirals winding in different ways. The later-formed vessels (*meta-xylem*) are usually the widest, and the lignin is deposited all over the inside of the tube except at a large number of minute areas. A vessel of this kind is said to be pitted (Fig. 97, *Pit*),

and it is necessary, if two vessels run alongside each other, for the pits in one vessel to be left opposite those in the other. The pits are not perforations, but only places where the original cellulose has not been thickened or only slightly so. In addition to the vessels, some long cells with fine-pointed

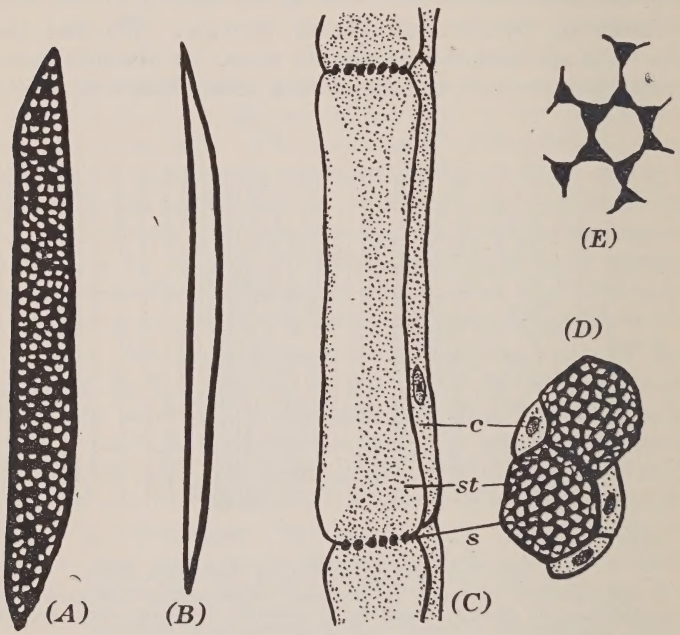

FIG. 98.

Longitudinal sectional views of a pitted tracheid of horse-chestnut (*A*), a wood fibre of horse-chestnut (*B*), and a sieve-tube of white bryony with companion cells (*C*). *D*, T.S. of sieve-tubes (*st*) with sieve-plates (*s*) and companion cells (*c*) of white bryony (protoplasm dotted). *E*, T.S. of collenchyma (white bryony). All × 367.

ends are lignified in a pitted manner and these *tracheids* (Fig. 98, *A*), as they are called, may help both in conduction and in the maintenance of rigidity.

The presence of thinner areas on the walls of developing vessels or tracheids is necessary for the increase in size and thickness of the cell-wall. In order for thickening to occur,

material must be brought to the protoplasm of the cells. If a tracheid is thickened evenly, the difficulties of food transport will become greater as the cell-wall becomes thicker. When thinner areas are left, the osmosis of the required substances, and also of waste substances, can take place through them and the protoplasm can remain in a state of activity. In the case of a vessel, which is continuous from the root to the stem, these thinner areas appear to be less necessary, since the material absorbed by the root is available. This material may, however, require to be supplemented by substances conveyed in the phloem, and these substances can only reach the vessels by osmosis through the thinner areas. During the formation of these vessels, the protoplasm gradually disappears, and fully-formed vessels are usually dead.

Wood Fibres and Parenchyma. In some of the long, sharp-pointed cells, thickening goes on till the pits are absent or almost so ; these dead cells can only serve for strengthening purposes, and are spoken of as wood fibres (Fig. 98, *B*). In addition to the three kinds of thickened cells, some ordinary cells are present. This wood parenchyma fills up any spaces between the thickened elements, facilitates transverse diffusion, and is often used for storage purposes. Intermediates between these different kinds of elements may also be found.

Cambium. Between the xylem and phloem there is a layer of actively dividing cells and this particular meristem is known as the cambium. The cells are more or less brick-shaped (Figs. 95 and 97, *Ca*), have thin walls and are usually smaller than the cells surrounding them. On the outer side, the cells formed by the activity of the cambial layer gradually alter to form some kind of phloem cell, whilst on the inner side they develop into the elements of the xylem. Theoretically there may be only one layer of meristematic cells, but the term cambium is often applied to all the thin-walled cells separating the xylem from the phloem.

Medulla. The pith or medulla (Figs. 95 and 97) consists of parenchymatous cells. The cells of the pith do not increase in number, but as the stem gets thicker they enlarge considerably. When the passage of material is insufficient to

allow for this increase in size to keep pace with that of the stem, the pith cells break down and a hollow stem results. The rays of parenchymatous cells, which lie between the fibro-vascular bundles, and join the parenchyma of the cortex with that of the pith, are termed medullary rays.

Stereom. The mechanical tissue (stereom) which gives rigidity to the stem is arranged in various ways (Fig. 99), and its arrangement largely depends on the needs and habits of the plant. In aquatic plants, a large amount of support is afforded by the surrounding water, and the stereom tissue

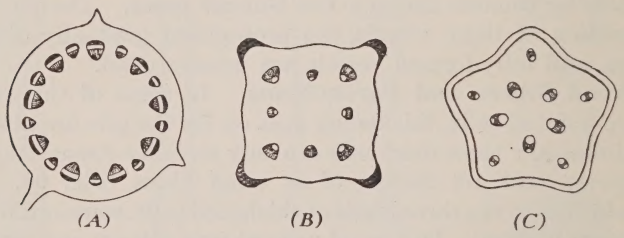

Fig. 99.—Mechanical Tissue (Stereom).

A, Helianthus. B, Lamium. C, Bryonia. T.S. of stems in which the parenchyma is left clear. The xylem of the fibro-vascular bundles is indicated by striation whilst the phloem is left clear. Note that internal phloem is present in the bundle of *Bryonia* (*Cucumis* is similar). In *Helianthus* the pericycle external to the bundle is thickened, and in *Lamium* the cells at the corners are collenchymatous.

is of a primitive or reduced character. When other structures are similar, the stereom tissue in the stem of an erect plant is much greater than when the stem is of a decumbent nature. It must be remembered that a considerable amount of rigidity can be attained in a parenchymatous tissue, owing to the pressure of the cells, when swollen with water, against each other. The distribution of stereom in three erect stems of different forms is shown in Fig. 99. The cylindrical stem of the sunflower (*Helianthus*) and the quadrangular stem of the dead-nettle (*Lamium*) depend entirely on the stereom for their erectness, but the irregularly pentagonal stem of the white bryony (*Bryonia dioica*) has the maintenance of its rigidity assisted by tendrils.

Older Stem of a Dicotyledon

It is a matter of common observation that parts of plants become woodier as they get older, and that plants which persist from year to year develop a woody stem. This is, of course, what may be expected, since an increase in the size of the plant will necessitate an increase in the supporting and vascular elements. For some time the extra needs of the plant may be met by the formation of new phloem and xylem due to the activity of the cambium in the fibro-vascular bundles (Fig. 95), but in woody plants this activity is supplemented by that of a layer of cells in the medullary ray.

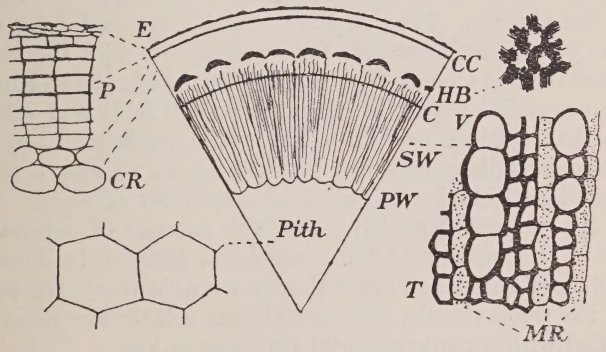

Fig. 100.—T.S. of Stem of a Dicotyledon with Secondary thickening. Horse-chestnut.

E, old epidermis; *P*, periderm or cork; *CC*, phellogen or cork cambium; *CR*, cortex, with intercellular spaces; *HB*, pericyclar caps; *C*, cambium; *SW*, secondary wood with medullary rays (*MR*), tracheæ or wood-vessels (*V*) and tracheids (*T*); *PW*, primary wood. Sector × 10; portions × about 150.

These cells have been, for some time, functioning as permanent tissue, but since little differentiation has occurred in them, they are still able to resume their former meristematic property. Owing to the re-assumption of activity in these cells, a ring of cambium is eventually formed. The original cambium within the bundles may be termed the *intrafascicular* cambium, whilst the secondary cambium is *interfascicular*. By the activity of this ring of cambium, a ring of secondary phloem is formed towards the outside and a ring of xylem on the inside (Fig. 100).

Secondary Tissue. Both secondary phloem and xylem are similar to the corresponding primary tissues in a younger stem, though there are none of the earlier-formed kinds of vessels in the xylem, all of them belonging to the pitted type. In consequence of the continued activity of the ring of cambium, the primary xylem and first-formed secondary xylem will be separated, further and further, from the phloem and the cortex, and difficulties in regard to food material will arise. To prevent this isolation of the xylem from the phloem, some of the cambial cells do not give rise to phloem or xylem, but produce parenchymatous cells forming radial rows, and therefore connecting the xylem with the phloem. These radial rows, like the medullary rays in the young stem, connect the outer tissues with the inner, and are termed secondary medullary rays (Figs. 100 and 101).[1] They are radial plates, often only one cell wide and seldom more than a dozen cells in height. The arrangement of one of these medullary rays can be imitated by driving a much flattened nail along the radius of a cylinder of wood. The cells are elongated radially, and the passage of substances between the outer and inner tissues is thereby facilitated; the phloem and other outer tissues are able to obtain water from the wood vessels, whilst the living cells in the wood are supplied with organic material from the phloem.

Annual Rings. During the spring, the wood elements formed by deciduous trees are larger than those formed in the autumn. This is partly due to the greater demand for water in the more active period of growth. As all cambial activity ceases in the winter, the circular zone of small autumn wood elements is succeeded by a zone of large spring cells and vessels. This gives an appearance of rings (Fig. 101) which can easily be seen by the unassisted eye, though the actual cells can only be seen with the aid of a strong lens. The number of rings will give the approximate age of the tree, and therefore they are called annual rings. Most of our deciduous trees show these annual rings, and their periods

[1] The term secondary is sometimes restricted to those rays which do not pass right through the secondary tissue.

of dormancy occur in the winter time when the leaves are lost. In some countries where defoliation occurs during the dry season of the year, rings may be formed, though it must be noted that the alternation of activity and dormancy does not correspond with spring and winter, but with the rainy season and the dry season. The number of rings does

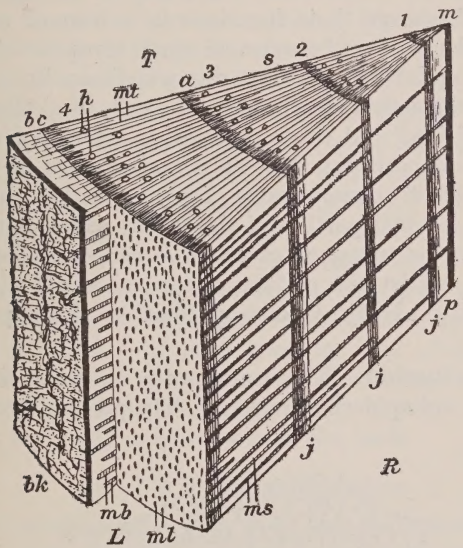

FIG. 101.—Annual Rings.

Portion of a four-year-old stem of the Scotch fir (*Pinus sylvestris*) cut in winter (× 6). (After Schenck.) *T*, transverse view; *R*, radial view; *L*, tangential view; *s*, spring wood; *a*, autumn wood; *m*, medulla; *p*, protoxylem; 1, 2, 3, 4, four successive annual rings; *mt*, *ms*, *ml*, medullary rays in transverse, radial and tangential views respectively; *mb*, medullary rays in phloem; *c*, cambium; *b*, phloem; *h*, resin canals; *bk*, bark external to the first periderm layer and formed from the primary cortex.

not always exactly correspond with the age of the tree; sometimes the differences between the spring and autumn elements may not be sufficiently marked, and the number of rings is less than the age of the tree. On the other hand, it is possible for more than one ring to form in one year. When the leaves are stripped off in summer and fresh leaves grow again during the same summer, two periods of great activity

occur, two lots of spring wood are produced, and two annual rings formed. In the countries where defoliation occurs during the dry season, two dry seasons in one year may cause two rings in that year.

Sap and Heart-Wood. As the stem gets older and increases in girth, there will be more and more squeezing of the cells against each other, and many of the cells will be unable to discharge their functions in a normal way. The primary phloem often becomes so much compressed as to be scarcely recognizable, and the earlier wood loses its conducting function and consists merely of dead mechanical tissue. The transport of food and waste material is interfered with, and the latter is deposited in the walls and cavities of the wood elements, which consequently become darker in colour. This darker central portion of the wood, which is no longer concerned in the transport of water, is called the heart-wood or *duramen*, whilst the peripheral region, which still retains its conducting ability, is distinguished as the sap-wood or *alburnum*.

Cork-Formation. There must also be great changes in the cortical and epidermal regions. The protective epidermis

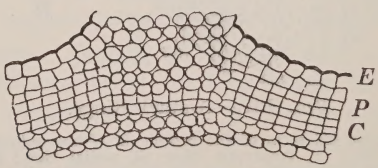

FIG. 102.—T.S. of Stem through a Lenticel.
C, cork cambium; *E*, epidermis with cuticle; *P*, cork.

becomes tightly stretched and finally splits, but before splitting occurs, a secondary epidermis is formed beneath the primary one, and the actual living cells are not exposed. This secondary epidermis (Fig. 100, *P*) is formed of different materials to the primary or original one, being formed of brick-shaped cork cells which are developed in the following

manner. A layer of cells within the epidermis becomes meristematic, and forms a *cork-cambium* (Fig. 100, *CC*) or *phellogen*. The active living cells of this phellogen divide, the cells formed gradually increase in size, and suberin is formed in their walls. They are thus rendered almost impermeable to water, and constitute the dead external layer of cork or periderm. The phellogen is usually one of the outer cortical layers but sometimes occurs further in, and then, besides the external cork, an inner lot of living cells, which functions as a secondary cortex or *phelloderm*, is produced.

Lenticels and Bark. Some areas of the cork-cambium do not give rise to rectangular cork cells but to spheroidal cells with cellulose walls and, as these areas are often lens-shaped, they are termed lenticels (Fig. 102). Air is able to pass through the intercellular spaces of this loose tissue so that they form a means of communication between the atmosphere and the internal tissues, and thus take on the function which the stomata performed in the primary epidermis. The formation of cork goes on year after year, the cork jacket splitting when it becomes too small, so that in an old stem many layers of dead cells are on the outside, and these are commonly known as the bark.

Stem of a Monocotyledon

In a monocotyledon (Fig. 105) we find that the same tissues are present as in a young stem of a dicotyledon, but there are differences in detail and in arrangement. The fibro-vascular bundles are not arranged at equal distances from periphery, but are scattered (Fig. 105, *A*) about in any part of the stele, so that there is no distinct medulla. In the dicotyledon, the strands of cells (*procambial strands*), giving rise to the bundles, differentiate into permanent tissue (phloem and xylem) on the outer and inner sides, but the middle cells remain undifferentiated and meristematic, as the cambium, and the bundle is *open* or capable of becoming larger. In the Monocotyledon, the procambial strands completely differentiate into permanent tissue (phloem and xylem). There is then no layer of cambium in the middle and the bundle

is incapable of becoming larger by the formation of new cells and is said to be *closed*. Secondary thickening and cork-formation cannot occur in the same way as in a dicotyledon, and, in fact, does not usually occur. The increase in girth of a monocotyledonous stem is due, not to an increase in the number of cells, but to an increase in their sizes, and many

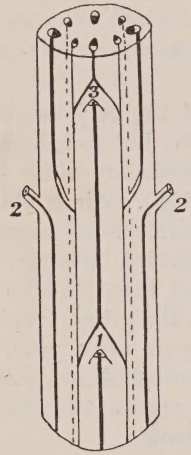

FIG. 103.—Longitudinal Course of the Bundle in a Dicotyledon.

Diagram (optical view) of the course of the vascular bundles in the stems of *Cerastium*. (After Prantl, slightly modified.) Only the leaf-bases of the opposite and decussate leaves are shown. The longitudinal courses of the postero-lateral bundles are indicated by dotted lines.

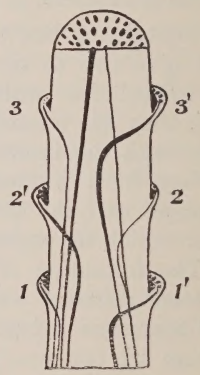

FIG. 104.—Longitudinal Course of the Fibro-vascular Bundle in a Monocotyledon. (After Prantl.)

Palm stem cut in half and leaves cut off above their insertions. The leaves are regarded as distichous and sheathing, and are therefore seen on both sides of the stem; the middle parts of their leaf-bases are at 1′, 2′, and 3′.

of the cells are large enough to be seen with the unassisted eye. In a few cases where secondary growth occurs, some groups of cells dedifferentiate and become meristematic so that extra bundles may be formed.

Longitudinal Course of Bundles. The longitudinal course of the bundles in the stem of a monocotyledon (Fig. 104) is different from that of the stem of a dicotyledon (Fig. 103).

The bundles from the leaf (leaf-traces) run obliquely downwards towards the centre of the stem and then curve outwards, and, after passing through one or more internodes, join on to bundles passing in from older leaves (Fig. 104). A transverse section at any level will therefore show a scattered arrangement of the bundles. In a dicotyledonous stem, the leaf-traces pass into the stem and run downwards parallel to

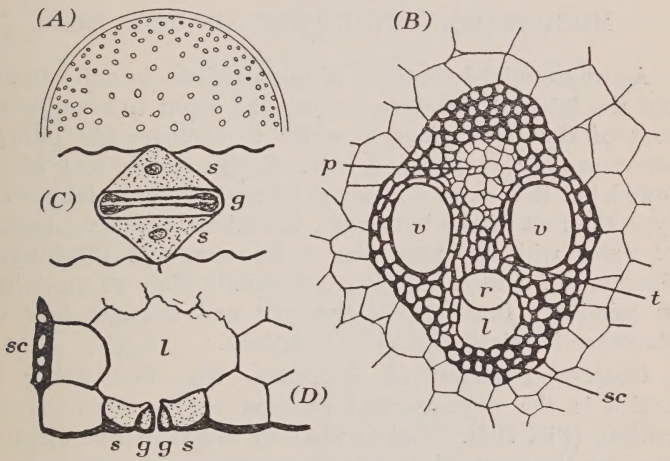

FIG. 105.—Stem of Monocotyledon.

A, T.S. of stem of maize (× 3) with many scattered bundles. *B*, fibro-vascular bundle with some of the surrounding cells (× 150). *v*, large pitted vessel; *r*, ring of annular vessel of protoxylem; *l*, lysigenous space where the protoxylem has broken down; *p*, phloem, with sieve-tubes and companion-cells; *sc*, sclerenchymatous cells surrounding the bundle; *t*, tracheids. *C* and *D*, surface and sectional views of epidermal cells of leaf showing a stoma. *g*, guard cells; *l*, air-space; *s*, subsidiary cells; *sc*, sclerenchyma.

the periphery. After passing through one or more internodes, they usually join with the bundles passing in from older leaves. The number of internodes which are passed through before a junction with other bundles is effected varies in different plants and the manner in which such junction is effected also varies. One method is shown in Fig. 103, where the bundle passes one node and bifurcates to join neighbouring bundles at the level of the next node.

CHAPTER XVI

MICROSCOPIC STRUCTURE OF THE ROOT

As we examined the stem of the artichoke in order to find out the internal structure, we perhaps ought to examine the root of the same plant in order to compare the internal structures of the stem and root. Such a course may be followed, but it is more convenient and advisable to take as our type the root of the buttercup, the microscopic examination of which will give us a general knowledge of the internal structure of a root. During our examination we must bear in mind the functions of the root and consider how the structure is related to these functions.

Central Position of Stereom. The first thing we notice is the more central position of the fibro-vascular portion (Fig. 106). This is what we might expect when we consider the mechanical uses of the two organs, especially as there are sufficient reasons for considering the central position of the fibrous tissue to be a primitive arrangement. The root is more or less supported by the soil and any rigidity required can be maintained by a core of thicker walled cells, but in the stem sufficient rigidity must be attained, in most cases, to enable an upright position to be maintained. This could, of course, be ensured by a sufficient number of thicker walled cells in the core, but we must also take into account that support is required for the leaves and this involves a strain on the peripheral portions. To provide for this the fibro-vascular bundles are placed near the periphery, the supporting mechanical tissue taking on the form of a hollow cylinder which is much stronger than a solid cylinder for the same outlay of material.

Alternation of Xylem and Phloem. Another important difference is in the arrangement of the phloem and xylem (Fig. 106). In the stem these are arranged so that the xylem is placed internally to the phloem along the same radius. In the root, although the phloem and xylem are side by side, they are not on the same radius, but side by side in a tangential

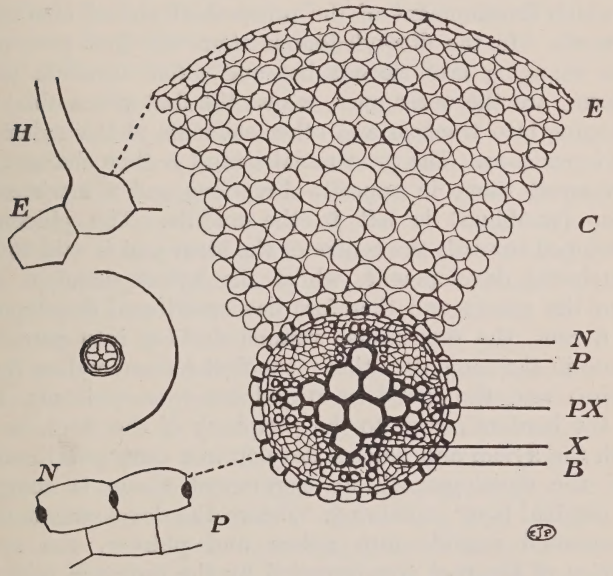

FIG. 106.—T.S. of Root.

Portion of root of buttercup (*Ranunculus repens*) (× 20 and × 100). Pith is present in a younger root. When the tangential walls of the endodermis become thickened thin-walled passage cells are left opposite the protoxylem. *E*, epidermis; *C*, cortex; *N*, endodermis; *P*, pericycle; *PX*, protoxylem; *X*, xylem; *B*, phloem; *H*, root-hair. Smaller portions × 300.

manner. The phloem and xylem originate in a similar manner to that described for the stem. Longitudinal strands of meristematic cells (procambial strands) are gradually altered, as the root gets bigger, so that the characteristic elements of phloem or xylem are formed, each pair of strands developing so that one becomes a phloem strand and the other a xylem

strand. A fibro-vascular bundle comparable to that of the stem is therefore considered to be represented by a neighbouring pair of strands; therefore a root is said to have three fibro-vascular bundles when it has three strands of xylem alternating with three strands of phloem.

Centripetal and Centrifugal Development of Xylem. There is, however, an important difference in the direction in which development of the procambial strand into xylem proceeds. In the dicotyledonous stem, the first procambial cells changing into sieve tubes and other elements of the phloem, are the outer ones, whilst the first procambial cells changing into tracheæ and other elements of the xylem, are the inner ones. The procambial strand is thus changed into permanent tissue in opposite directions and a meristematic layer (cambium) is left in the middle. The phloem is developed towards the centre of the stem and is said to have centripetal development, whilst the xylem develops away from the centre and therefore has centrifugal development. In a root, the procambial strands develop into permanent tissue in the same direction; the first-formed xylem (protoxylem) and the first-formed phloem (protophloem), being on the borders nearer to the periphery of the stem, so that both the xylem and phloem develop in a centripetal manner, and the development into permanent tissue is complete, no cambial layer remaining. Before the development of the procambial strands into xylem and phloem, the central portion of the root was occupied by the ordinary parenchymatous cells of the pith, but afterwards the xylem may encroach on the central portion so much that little or no pith is present in the mature root. The number of bundles in the root of a dicotyledon is usually from two to five, whilst in that of a monocotyledon, the bundles are more numerous, and the large xylem vessels often have a more circular outline (Fig. 109).

Epiblema. The outer tissues have a similar arrangement as they have in the stem (cf. Figs. 95 and 106). The outermost layer may be the original epidermis, or it may not. During the penetration of the root into the soil the original

epidermis may have been rubbed off, so the non-committal term of epiblema or piliferous layer is sometimes used for the apparent epidermis. A cuticle is present for protective purposes and in the younger parts of the root (except the root-tip) some of the epidermal cells elongate more or less at right angles to the axis and form thin-walled root hairs. At the root-tip the epidermal cells become more than one layer thick and form a cone of boring cells constituting the root-cap. No stomata are present as the root is not concerned with transpiration or photosynthesis.

Cortex. This is relatively much thicker than in the stem and is much less differentiated (cf. Figs. 95 and 106). Its cells are thin walled, usually contain numerous starch grains, and inter-cellular spaces for the diffusion of gases are present. The innermost layer (endodermis) of the cortex is usually much better defined and more strongly thickened than in the stem. It consists of brick-shaped cells each having a peculiar thickening (**Casparian strip**) winding round it. In transverse sections this ribbon causes the middle portions of the radial walls to appear thicker (Fig. 106, *N*) than the end portions. The stele of the root is therefore more definitely separated from the cortical cylinder and the pressures in the two parts may be different. We may then regard the endodermis as a limiting layer separating a region of low pressure, the aerating tissue of the cortex, from a region of high pressure, the water conducting tissue of the stele. When extensive thickening of the endodermis occurs at an early stage, some endodermal cells opposite to the xylem strands remain thin-walled, and serve as passage or transfusion-cells (Fig. 109, *C*).

Stele. This consists of three groups as in the stem, but, as we have seen, the phloem and xylem are arranged in a different manner and the pith in an older root is often obliterated. The pericycle, as in the stem, is the portion between the endodermis and the ring of fibro-vascular bundles and intervening parenchyma. It is usually a single layer in the root and it is from cells of this layer that lateral roots originate (Fig. 107). The development of the young root is therefore said

to be endogenous and it must be noted that the cells external to it must be absorbed as the root penetrates to the exterior. The cells outside the developing root secrete a ferment, a little digestive sac is formed and the cortical cells are disorganized (Fig. 107); thus, not only is a passage made for the young root, but nutritive substances are supplied to it. In the stem, lateral branches are formed from protuberances of the outer tissues only, and they are therefore said to be

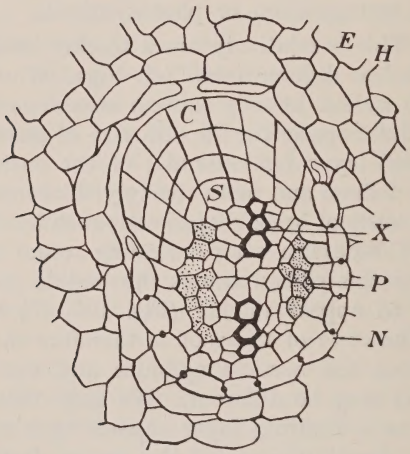

FIG. 107.—Development of a Lateral Root in a Phanerogam.

T.S. of *Teesdalia nudicaulis* (after van Tieghem) (× 300). *E*, epiblema with root-hairs (*H*); *N*, endodermis; *C* and *S*, developing cortex and stele of lateral root; *X* and *P*, xylem and phloem of parent root.

developed exogenously. When adventitious roots are formed on the stem they originate in the pericycle and develop similarly to normal roots.

Secondary Thickening. As no cambium remains from the original procambial strands, the method of secondary thickening is different from that of the stem at the beginning; though, later on, the xylem and phloem elements increase as in the stem. The cells internal to the phloem become meristematic, producing phloem on the outside and xylem on

the inside, and the cambium ring is then completed from the cells of the pericycle outside the primary xylem. This cambium ring must then at first be uneven, forming bays internal to the phloem and promontories external to the xylem, but, owing to its continued activity, the wavy outline gradually disappears and then the formation of secondary tissue is similar to that of the stem. It is therefore difficult to distinguish between an old root and an old stem, though it is possible to do so by noting the position of the protoxylem in the primary strands.

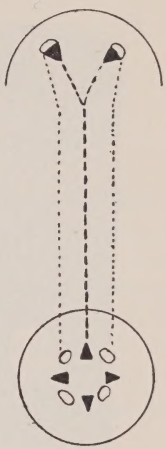

Fig. 108. — Diagram to show one kind of Transition from the Vascular Structure of the Root to that of the Stem.

The clear areas indicate phloem whilst xylem is represented as dark. The semicircle represents half of the stem as seen in transverse section. The circle represents a T.S. of the root. The xylem strands from the laterally-placed xylem of the root are not indicated in the figure though they contribute to the xylem shown in the stem.

Phellogen. When secondary growth goes on for a considerable time, cork-formation occurs as in the stem, though the cork-cambium is always deep-seated (the pericycle becoming completely meristematic) and phelloderm is consequently produced.

Secondary Thickening in Monocotyledon. In a Monocotyledon there is usually no secondary thickening, though both secondary vascular and epidermal tissues may arise in those plants (e.g. *Dracæna*) which show a kind of secondary thickening in the stem.

Transition between Root and Stem. As the xylem and phloem of the root are respectively continuous with the xylem and phloem of the stem there must be an intermediate portion where a transition (Fig. 108) occurs between root and stem structure. The transition occurs in various ways and two of the main methods may be given as examples. In one method the phloem strands follow a straight course from the root to the stem whilst the xylem strands divide.

In this case the xylem in the bundle of the stem is derived from the halves of two xylem strands in the root. In the second method the xylem strands follow a straight course whilst the phloem strands divide, and so the phloem in the

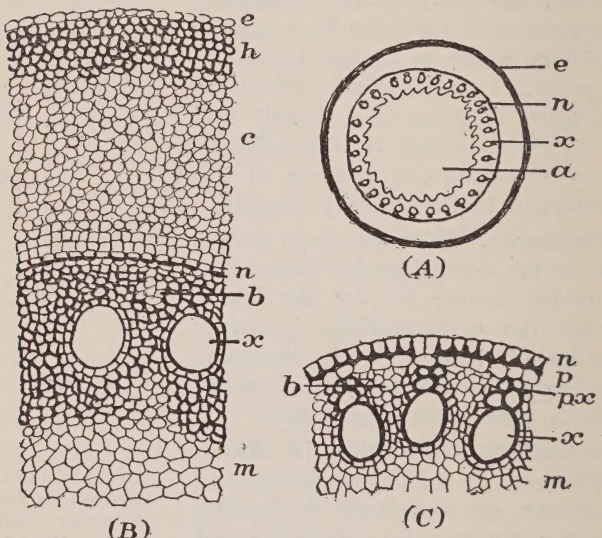

FIG. 109.—Root of Monocotyledon.

A and *B*, T.S. of root of maize (× 7 and 65 respectively). *C*, portion of T.S. of root of *Iris pseudacorus* (× 100). *a*, air-space; *b*, phloem; *c*, cortex; *e*, epiblema; *h*, hypodermis; *m*, medulla; *n*, endodermis with two thin-walled passage-cells opposite the protoxylem of the median xylem group; *p*, pericycle; *px*, protoxylem; *x*, large wood vessel.

bundle of the stem is derived from two phloem strands in the root. In both methods the xylem must rotate through 180° as the protoxylem in the stem is on the medullary side whereas, in the root, it is on the side towards the cortex.

CHAPTER XVII

INTERNAL STRUCTURE OF A LEAF

In most flowering plants the upper surface of the leaf is different from the lower surface. Such a leaf is known as a bifacial or dorsiventral one, and its internal structure must be considered before that of any other kind. The leaf selected for sectioning and examining under the microscope may be that of the artichoke, though a stiffer and thicker leaf, like that of the holly, is easier to manipulate. The following description applies to the leaf of the holly, or to almost any other *bifacial leaf* of a dicotyledonous land-plant.

The leaf is a flattened expansion with veins for conducting purposes and the main veins are more prominent on the under and paler surface. The difference of colour between the two sides of a leaf is due to the preponderance of chlorophyll towards the upper surface.

Epidermis and Stomata. The upper surface (Fig. 110, *E*) is covered by an epidermis of more or less dead cells which therefore acts as a protective layer. The lower surface also has an epidermis (Fig. 110, *U*) but usually the two epidermes are slightly different. The lower epidermis is on the more shaded side and the cuticle is thinner, as there is less need for protection against undue evaporation. Provision must also be made in a cuticle-protected leaf for the entrance and exit of gases, therefore minute openings (stomata) are left. In most dorsiventral leaves these openings are confined to, or more abundant on, the under surface (Fig. 111) which, as experiment has shown us, is the surface which gives off most water. A little consideration will convince us that the

under surface is much better than the upper one for these transpiring pores, as transpiration will be much more regular there than on the more exposed upper surface. The temperature and humidity of the atmosphere will also influence the amount of water-vapour transpired and there ought to be some means of regulating the size of the pores. Round each pore two of the epidermal cells (guard-cells) become more or less semilunar in shape (as seen in surface view), retain their protoplasm and chlorophyll, and are able to alter the size of the opening (Figs. 105 and 111). The guard-cells are

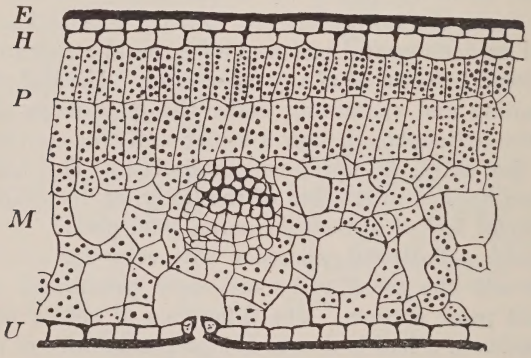

Fig. 110.—T.S. of Leaf of Holly.

E, upper epidermis with thick cuticle. *H*, hypodermis. *P*, palisade parenchyma of mesophyll containing chloroplasts. *M*, spongy mesophyll with air-spaces and a fibro-vascular bundle (cut transversely) with the xylem towards the upper surface. *U*, lower epidermis with stoma and guard cells.

seldom flush with the surface of the leaf, being usually placed a little below the ordinary epidermal cells. This protected position tends to make transpiration more regular. The actual openings are minute but they are usually very numerous, a square millimetre often containing more than 200. The escape of water-vapour from these numerous stomata is quite as great as from a free surface, so that the formation of a cuticle, which is perforated by stomata, does not hinder the loss of water-vapour when the stomata are open, though it

provides an excellent means for controlling transpiration by partial or complete closing of the pores.

Mesophyll. The tissue between the two epidermes is known as the mesophyll (Figs. 110 and 149) and in it we find larger and smaller veins running in all directions, each vein containing xylem and phloem elements which are continuous with those of the stem. As the xylem and phloem pass from the leaf into the stem without twisting, the xylem must lie toward the upper surface of the leaf and the phloem towards the under surface. Endodermal and pericyclar cells are present in the larger bundles; the former often containing starch and the latter often becoming lignified.

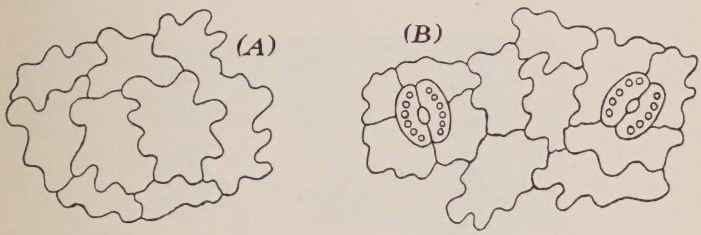

FIG. 111.—Epidermal Cells of the Ivy-leaf.

A, upper surface without any stomata. *B*, lower surface with stomata, each surrounded by two guard cells containing chloroplasts.

Palisade Tissue. The mesophyll below the upper epidermis of the leaf consists of one or more layers of narrow cylindrical cells having the appearance of a palisade, hence it is called palisade tissue.[1] These cells contain numerous chloroplasts, fit together fairly closely, though some intercellular spaces occur, and perform most of the photosynthetic work of the plant. The leaf becomes a deeper green in the shade than when strongly illuminated. During bright sunlight the chloroplasts arrange themselves at the sides or towards the bases of the palisade cells, whilst in diffuse

[1] In the holly an extra layer of thickened cells, which may be called the hypodermis (Fig. 110, *H*), intervenes between the epidermis and the palisade cells.

light they are nearer to the upper surface of the leaf. The shape of the chloroplasts may also alter so that with increased illumination they become smaller and thicker whilst in weak light they become flattened out. These phototactic movements and alterations in shape of the chloroplasts enable the optimal amount of light to be obtained, and tend to protect the contained chlorophyll from the destructive influence of excessive light.

Below the palisade tissue the mesophyll consists of irregularly shaped cells containing fewer chloroplasts and

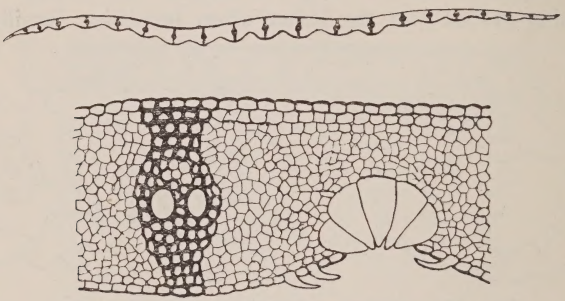

FIG. 112.—T.S. of the Leaf of a Grass (*Molinia cœrulea*).

Bars of sclerenchymatous cells are present and surround the fibro-vascular bundle. On the under surface of the leaf large triangular cells are present; when these are turgid, the leaf is straightened out, but when they lose water, the under surface of the leaf becomes smaller and the whole leaf consequently rolls inwards. Upper figure × 5, lower × 90.

with many air-spaces between them. This is appropriately called **spongy parenchyma**; its cells help in the process of photosynthesis and the spaces allow for the passage of gases, one large air-space usually being beneath a stoma.

Isobilateral Leaves. Many leaves, especially those of monocotyledons, do not set themselves at right angles to the incident rays of light, but have a more or less erect position, and a bifacial character is not developed. Such an isobilateral leaf has similar epidermes and any differentiation of the mesophyll is fairly even on both sides. In grasses and many other monocotyledons the vascular bundles are bridged

with the epidermes by means of intervening sclerenchyma (Fig. 112) and the leaf is thereby strengthened. Another interesting structure shown by the leaves of many grasses is that which enables the leaf to inroll. In *Molinia cœrulea* (Fig. 112) large triangular cells are present in furrows on the under surface. When the leaf is well supplied with water, these cells are turgid or swollen out and the leaf is flat, but when water becomes scarce these cells are the first to lose it and the leaf rolls up.

Centric Leaf. In some monocotyledons, e.g. onion, the leaf is similar on all sides and is then said to be a centric one. Its internal structure is also similar on all sides (cf. Fig. 148).

CHAPTER XVIII

DEVELOPMENT OF THE FLOWER-PARTS

All the different parts of the flower arise from small groups of meristematic tissue (primordia) at the top of the flower stalk. In the general order of things the primordia which first appear are those of the sepals, then in order appear the primordia giving rise to the petals, stamens and carpels. If the primordia of all the various parts develop independently of each other the sepals, petals, stamens and carpels are separate structures and this is what happens in flowers such as the buttercup. In many flowers independent growth of all the primordia does not occur and so we may get some of the parts joined together. In the campion the primordia of the sepals develop together, at any rate for some time, so that a gamosepalous calyx is produced. In the primrose the primordia of the petals also become confluent and a gamopetalous corolla is produced as well as a gamosepalous calyx. In the broom and mallow the stamens for some time develop together, so that the filaments are joined and the flower

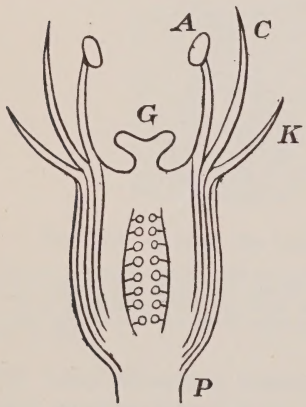

FIG. 113.—Diagram to show the Production of an Inferior Ovary.

The primordia of the sepals (*K*), petals (*C*), and stamens (*A*) have become confluent and grown up together. *G*, stigmas; *P*, pedicel.

is **monadelphous.** In a large number of plants the primordia of the carpels develop so as to form a syncarpous ovary. Some confluence between the primordia of different whorls of the flower also occurs and in this way epipetalous stamens, gynostemia (see p. 122), etc., are formed. The primitive position of the pistil is above the andrecium, corolla or calyx, but in many cases (e.g. willow herb) the ovary is inferior owing to the upward growth of the confluent primordia of the outer parts of the flower (Fig. 113).

Development of Stamen. The stamen arises as a little protuberance of meristematic tissue on the thalamus. By

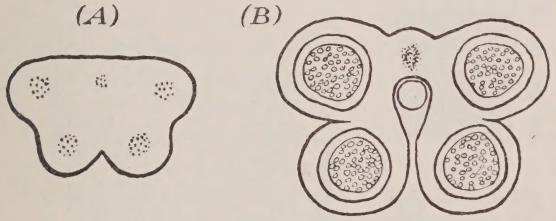

FIG. 114.—Stamen.

A, T.S. of a young stamen. The four developing pollen-sacs indicated by dots. The central lot of dots represent the developing vascular bundles (× 60). *B*, T.S. of older stamen of *Lilium* with pollen-sacs containing pollen grains and surrounded by disorganized tapetum. The cylindrical filament is cut through transversely and appears as a circle in the centre (× 12).

the division and increase in size of these cells the protuberance elongates, the lower portion becoming the filament whilst the upper part forms the anther. The details of the differentiation into filament and anther vary in different plants, according to the way in which the anther is fixed on the filament, and also in accordance with the respective sizes of the two parts, but usually the filament elongates after the anther has become differentiated, and then its vascular bundle is developed to carry food to the ripening anther. A transverse section of a young anther (Fig. 115, *A*) at the level where it joins the filament, shows that it consists of a more or less rectangular mass of parenchymatous cells, with a conducting strand towards the middle, four groups of meristematic tissue at

the rounded corners, an epidermal layer, and a slight depression indicating where the future division into two anther-lobes will occur. The chief cells which concern us are the four groups of meristem which develop into the pollen-sacs. Division and differentiation occurs in these, so that in many cases we have three layers of cells formed outside the cells (**archesporium**) which will produce the pollen-grains. The outer layer which is just beneath the epidermis of the anther is the fibrous layer consisting of cells strengthened by the development of fibres, the inner layer is called the **tapetum**

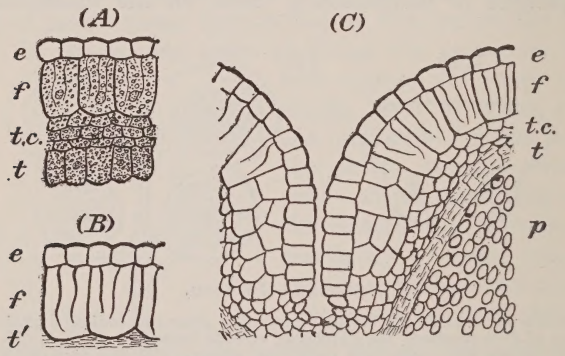

FIG. 115.—Anther.

A, portion of T.S. of young anther; *e*, epidermis; *f*, fibrous layer; *t.c.*, transitional cells; *t*, tapetum. *B*, portion of T.S. of old anther; *t'*, remains of transitional cells of tapetum. *C*, section of a nearly mature anther (*Lilium*) at place of dehiscence between the two pollen-sacs in one anther lobe. The fibrous layer thins out and the tapetal cells are disorganizing; *p*, pollen grains in pollen sac (× 75).

whilst the intermediate layer (which may consist of several rows of small cells) is the **transitional epithelium** (Fig. 115, *A*). The fibrous layer is the wall of the pollen-sac and thins out (Fig. 115, *C*) where dehiscence of the anther will take place, and the transitional and tapetal layers become disorganized (Figs. 114 and 115) during the division of the archesporial cells.

Formation of Pollen. The cells of the archesporium divide to form pollen-mother-cells and each of these divides to form four pollen grains. In Dicotyledons the nucleus of

each pollen-mother-cell divides, then each nucleus divides again so that there are four daughter nuclei in the same envelope, and finally limiting walls of cellulose are laid down so that four pollen-grains are formed, each having a delicate inner wall (endosporium) and a stronger outer wall (exosporium). This method of cell-formation in which the nuclei divide into the full number before cell-walls are laid down is known as free-cell formation. In Monocotyledons the four pollen-grains are not produced by free-cell formation. The nucleus of the pollen-mother-cell divides and then cell-walls are developed before the nuclei divide again.

Pollen-Tube and its Contents. Each pollen-grain is uninucleate (Fig. 93, *A*, *B* and *C*) at first, but before it leaves the anther its nucleus and protoplasm divide into two cells, one of which is a small generative cell surrounded by a cell-wall (Fig. 93, *D*) and lying freely in the larger vegetative cell, the former being the cell actively concerned in reproduction whilst the latter is a more passive agent as it merely provides food for further development. Before or after pollination the generative cell divides into two cells (Fig. 93, *E*), but cell-walls are not formed. These two naked generative cells are the male cells or gametes capable of stimulating the egg-cell or female gamete of the ovule. The pollen-grain after its conveyance to the stigma takes up moisture, swells out and the exosporium is ruptured, the rupture usually occurring at special areas where the exosporium is thinner. The endosporium protrudes and forms a fine tube (Fig. 93, *F*) which grows down the style to the micropyle of the ovule.[1] The definite path taken by the pollen-tube is not due to geotropism or heliotropism or hydrotropism but is determined by the chemical stimulus of some substance (e.g. sugar) present in the cells of the style, so that this kind of sensitiveness or irritability is known as **chemotropism** or **chemotaxis.**

Development of the Ovule. In each carpel one or more ovules develop and the particular portion from which the development occurs is known as the **placenta.** In syn-

[1] In some cases, e.g. hazel, birch, the pollen tube pierces the base of the ovule.

carpous ovaries the placentas may be on the walls of the carpels (parietal placentation) as in the violet (Fig. 116, *B*), or they may be near the centre. When the central column is joined by walls to the wall of the ovary the placentation is axile (e.g., bluebell, Fig. 116, *C*), but when the column is free from the periphery of the ovule the placentation is free-central (e.g. primrose, Fig. 116, *A*).

The ovule arises as a tiny cellular protuberance on the placenta and this grows larger, not only by the formation of fresh cells, but also by the enlargement of the cells. From

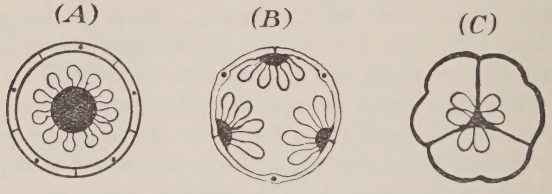

Fig. 116.—Placentation.

Diagrammatic T.S. of ovaries. The placentas are shown dark, the ovules in outline only. In *A* and *B* the main vein in the middle of each carpel, and the divisions between the carpels, are indicated. *A*, free-central placentation of primrose with 5 carpels. *B*, parietal placentation of violet with 3 carpels. *C*, axile placentation of bluebell with 3 carpels.

the base (**chalaza**) of this protuberance (nucellus) one or more coverings or integuments are formed in an apical direction whilst growth in a basal direction gives rise to the stalk or **funicle** of the ovule. In some cases (e.g. dock) development proceeds so that the micropyle is directly opposite to the stalk and the ovule is said to be **orthotropous** (Fig. 94, *A*), but in most cases the funicle is attached to the side of the ovule, which thus appears to be upside down, and is then said to be **anatropous** (Fig. 94, *B*). In many members of the mustard and cress family the orientation of the stalk to the micropyle is intermediate between these two conditions.

Rudimentary Structures. The formation of the egg-cell (oosphere) in the ovule is given in the chapter on fertilization, though no mention is made there of some divisions which occur in the cell near the micropylar end before it becomes

the embryo-sac. These seem to indicate that the embryo-sac is homologous to the pollen-grain. The hypodermal cell near the micropylar end may divide into four potential embryo-sacs, only one of which develops into the actual embryo-sac. This seems to be similar to the division of the pollen mother-cell into four pollen-grains. An earlier division of the micropylar cell into two seems to be a relic of an ancestral condition. The upper one is reminiscent of the tapetum of the pollen-sac whilst the lower one is the archesporium which ultimately forms the embryo-sac or megaspore. The full significance of such traces or relics cannot be appreciated without a knowledge of the life-history of the fern and of the theory of evolution. They are the rudiments or traces of structures which were formerly used by some ancestor of the plant.

CHAPTER XIX

SPECIAL METHODS OF FEEDING

The normal methods by which the higher plants obtain food have already been considered. The root-hairs take up dilute solutions whilst the leaves and any other part of the plant which contains chloroplasts take in carbon dioxide from the air. By these means the elements necessary for the nutrition of the plant are obtained; with the help of light the cells are able to build up all the substances present in them, and the plant is able to grow, not only by the formation of fresh cells but also by the increase in size of the cells.

General Methods in Cryptogams. In the lower plants such as mosses and algæ the same methods are employed though it may not be necessary for root-hairs to be present. The mosses have no true roots and therefore cannot have true root-hairs, though hairs (**rhizoids**) springing from the stem, not only fix the plant to the soil, but also take up the necessary water with salts dissolved in it (Fig. 175, *A*). In many cases a certain amount of absorption can be performed by the stem and leaves when they come in contact with dilute solutions as the cell-walls are seldom thick enough to prevent osmosis taking place. In algæ (Figs. 191–200) there are no real root-hairs and absorption of dilute solutions can occur at any surface which is exposed to such solutions, so long as the cells at that surface have thin walls. The absorption of carbon dioxide is carried on in the same manner in these lower plants as in the higher plants, though it must be remembered that many of them live in moist places. Some may be actually immersed in the water, and then carbon

dioxide, as well as any other substance required by the plant, will be absorbed from its solution in water.

Plants Submerged in Water. Some of the flowering plants which live in water may also absorb all or part of their nourishment from the water. Such plants as the Canadian

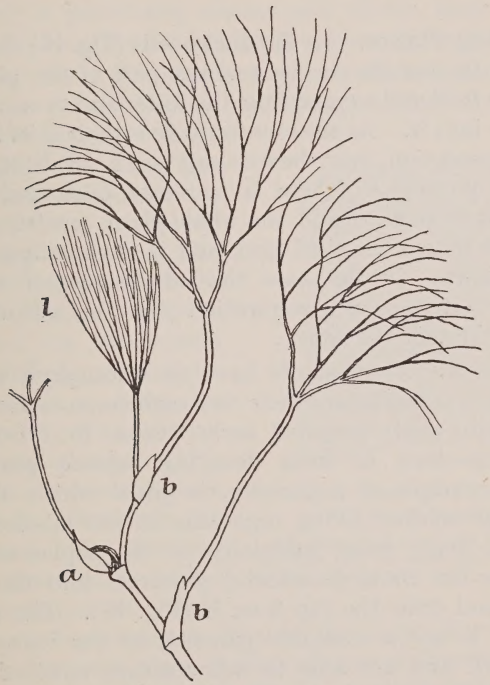

FIG. 117.—Submerged Leaves of Water-crowfoot.

At *a*, the tips of the divisions of a young leaf are still enclosed in the tip of the sheathing leaf-base; *b*, leaf-base; *l*, young leaf in which the divisions are still close together.

pond-weed, water-milfoil, water-violet and water-crowfoot, have their submerged leaves (Fig. 117) finely cut into slender filaments which present a large surface for the purpose of absorption. It must also be noted that respiratory exchanges are made in these plants through the medium of the water,

so that we have water-plants as well as water animals, which are dependent for their supply of oxygen on that dissolved in water. Some species of water-crowfoot have floating renate leaves in addition to the submerged finely divided ones, and as these leaves have stomata on the upper surfaces normal methods of respiration and carbon-assimilation are partially used.

Floating Plants. In the duckweeds (Fig. 16) the leaf-like fronds float near the surface and any part of the plant is able to obtain food and oxygen from the water and to excrete waste products into it. As the roots only float their chief function is that of absorption, even the root-cap (see p. 28) being modified for that purpose.[1] There is one rare duckweed (*Wolffia*) which has no roots at all: the whole plant consists of a little grain less than a mustard seed, and is the smallest flowering plant known. In this case the interchange of substances both for nutrition and respiration must be almost entirely effected through the water.

Parasites. Many plants have no chlorophyll and therefore cannot manufacture their own carbonaceous food. They may obtain ready-prepared carbonaceous food from actual living organisms or from decaying organic products. A familiar example of a parasite, or plant which obtains its food from another living organism, is the mistletoe which grows on many trees, especially on the poplar and apple. Its sucker-like roots (haustoria) penetrate into the wood of its host and draw the sap from it (Fig. 18). The mistletoe, however, is not a complete parasite, as the leaves contain chlorophyll and are able to manufacture most of the carbonaceous food required. The dodders which twine round clovers, gorse, heaths, and occasionally over many other plants, are more complete parasites, though a little chlorophyll is present in the stem. The dodder seed on germinating

[1] More direct interchange with the air is possible from the upper surface of the frond when this is at the level of the water, as in the common duckweed, though stomata are rare or absent in this particular plant. *Lemna gibba* has larger cells beneath and these are chiefly concerned in absorption.

at first forms a root and feeds for a short time like a normal plant whilst the apex of its shoot performs movements as though it was attempting to climb round some support. If it meets with its host, **suckers** or **sinkers** (Fig. 118) are formed and the dodder then obtains its nourishment from the tissues of its host. The broomrapes have leaves in which chlorophyll is practically absent and obtain their nourishment by sending haustoria into the roots of the host-plant.

Saprophytes. Plants which obtain their food from the decaying products of other organisms are known as saprophytes, and many of them are familiar to us. The mould which whitens a boot which has been neglected in a damp cupboard, the fungus which covers stale bread or cheese with a green coat, the mushrooms and toadstools growing on rotting wood or dung, are all plants in which chlorophyll is absent and in which the organic food-substances required are taken from the substratum of decaying matter. Amongst the higher plants examples of saprophytism are less common than in the lower forms of plant life, but there are some British species of flowering plants in which the food is obtained in a saprophytic manner. The birds-nest (*Monotropa*) and some orchids as the birds-nest orchid (*Neottia*), coral-root (*Corallorrhiza*) and *Epipogium* grow amongst decaying leaves. They are all leafless or have their leaves reduced to brown scale-like bodies, and it may be considered that they obtain their food from the organic substances formed by the decay of the leaves which have fallen from the neighbouring trees, though it is much more probable that a fungus acts as an intermediary, feeding on

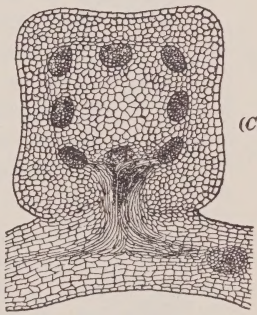

FIG. 118.—Section of Dodder parasitic on a Dicotyledon.

The stem is cut through transversely in the host (*C*), but somewhat longitudinally in the parasite (*D*).

the dead leaves and giving up its store of organized food to the flowering plants.

Insectivorous Plants

There are also some plants which are said to be insectivorous or carnivorous since they catch small animals and utilize their organic nitrogenous material. The most familiar examples among British plants are the sundews.

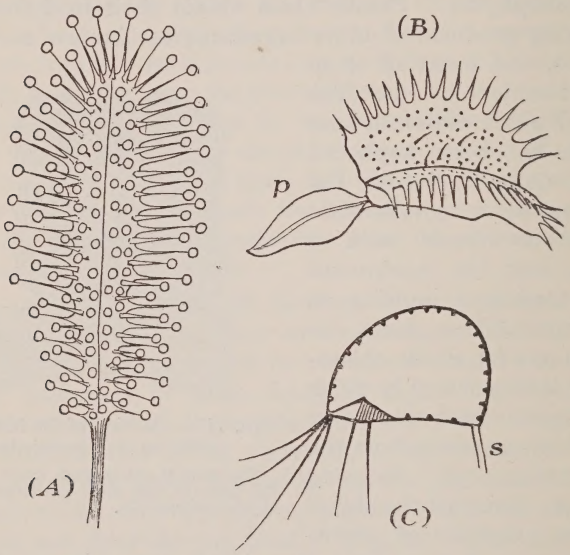

Fig. 119.—Carnivorous Plants.

A, leaf of sundew (*Drosera anglica*) in its expanded condition (× 2). The round leaved sundew has a more circular leaf. *B*, leaf of Venus' fly-trap. Three sensitive hairs are shown on the upper half of the leaf-blade (× 3). The digestive glands are represented by dots. The distal portion (*p*) of the petiole has become foliaceous in order to compensate for loss of leaf-surface. *C*, diagrammatic section of bladder of bladderwort (*Utricularia*) (× 13). *s*, stalk of bladder. The mouth, trapdoor, and hairs are at the other end from the stalk. The dots on the inside of the wall represent glands.

Sundews. These are small plants which grow in boggy places, sometimes right in the midst of a clump of bog-moss (*Sphagnum*), but more commonly at the margin. Their leaves (Fig. 119, *A*) are studded with a number of reddish hairs, each crowned with a glandular knob, which exudes a

sticky juice, and so the leaf appears to be covered with minute drops of dew. When an insect comes in contact with these sticky knobs the leaf is stimulated to curl over the intruder so as to form a digestive cavity. Then the glands pour forth a digestive juice containing substances similar to those found in the stomachs of animals and the body of the insect is digested, i.e., changed into substances which are soluble and capable of being absorbed by the process of osmosis. During the course of a few days digestion and absorption is completed, the leaf opens out once more and the indigestible remains (legs and wings) are blown away. We have three species of *Drosera* in the British Isles, the commonest being the round-leaved sundew. The Butterwort is another British plant which has a similar method of obtaining nitrogenous food though the glands are not so conspicuous and the leaf merely rolls round at the margin to form the digestive cavity (Fig. 120).

FIG. 120.—Leaf of Western Butterwort.

The margin is inflexed over three small flies.

Bladderwort. The Bladderwort (*Utricularia*) adopts a different device for capturing its prey. It is a plant which is completely immersed in water except for its yellow blooms. As usual in such immersed plants the leaves are finely divided and in addition are provided with small bladders (Fig. 119, *C*). Each of these bladders is provided with a trap-door which easily opens inwards but is very difficult to open from the inside of the bladder. Round this entrance to the bladder are a number of fine sensitive hairs, and when these are touched by a little crustacean or other minute aquatic animal, the trap-door opens and the animal is drawn into the cavity. Escape is almost impossible and the little prisoner dies in its jail, its decaying substances being used by the plant for food.

Pitcher-Plants. Some foreign plants, which are occasionally seen in our greenhouses, exhibit other methods by which the animal is captured. In the pitcher-plants part

of the leaf is modified into a pitcher into which insects fall. In the simplest kinds of pitcher-plant, the pitchers contain water which drowns the insects and then the products of their decay are utilized by the plant. In the true pitcher-plants (*Nepenthes*), the distal portion of the leaf expands into a pitcher, on the inner surface of which are digestive glands, whilst part of the leaf-blade is modified into a lid which prevents water falling in and weakening the digestive fluid (Fig. 121). The rim of the pitcher has a very smooth surface, and just inside this, honey-glands are present. Insects are enticed by the honey, slip on the very smooth rim, fall into the pitcher and are digested by the organic acids and the ferment pepsin.

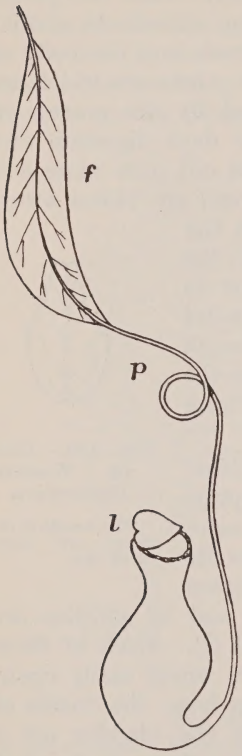

FIG. 121.—Pitcher-plant.

Pitcher of *Nepenthes*. *p*, petiole, becoming foliaceous (*f*) at its proximal end; *l*, part of lamina forming a lid over the mouth of the pitcher.

Venus Fly-Trap. In the Venus fly-trap the margins of the leaf are fringed with long bristles whilst the surface is provided with digestive glands and six sensitive hairs (Fig. 119, *B*). When a sensitive hair is touched by an insect twice in quick succession, the leaf closes up quickly and a digestive chamber is formed. The stiff bristles at the margins of the leaf do not interlock very closely, so that if the insect is too small for a substantial meal, it is able to escape.

Water-Cup of Teasel. Many other plants are known which have sticky glands on their leaves in which small insects become caught, but though they are sometimes known as fly-catchers they do not use the captured insects for feeding purposes. The common teasel has the bases of its leaves joined

together to form a water-cup, and it is probable that animals are drowned in this receptacle and the products of their decay used as food.

Symbiosis

Reference must be made in this chapter to symbiosis, though this is not always connected with special methods of feeding. Some plants are able to live closely connected so as to form a mutual help association in which both partners are assisted in their work. The roots of leguminous plants (clover, lupin, bean, etc.) have **nodules** or **tubercles** on them and the cells of these nodules have been shown to contain minute bacteria (*Bacillus radicicola*) which have the power of converting the free nitrogen of the air present in the interstices of the soil into nitrites and nitrates. This symbiosis is useful to both partners. The bacteria are usually rod-like in shape, are devoid of chlorophyll and cannot manufacture their own starchy food which is therefore supplied to them by the leguminous plant. On the other hand, the leguminous plants profit from the nitrates manufactured by the bacteria.

As the soil on which a leguminous crop is grown becomes richer in nitrates, such a crop is introduced by the farmer in his rotation of crops. It has been known for a long time that it was not an economical proceeding to grow the same crop continuously in the same ground. A corn crop and a root crop were alternated as they did not extract the same substances from the soil. For many years it has been the usual practice to introduce a leguminous crop so that there was a three-year rotation instead of a two-year one. Nowadays, as the requirements of the plant have been better ascertained by water culture methods and chemical analysis, it is possible for the farmer to grow what crop he pleases so long as he adds the necessary ingredients to the soil, though it is usually more economical to have a rotation in which a leguminous crop is used.

Mycorhizæ. The roots of many of our trees and shrubs (e.g. pine, ling) have been shown to be in close relationship with the filaments of fungi (*mycorhizæ*), and it was at first

thought that these fungi were merely parasitic on the larger plants. It has, however, been established that the mycorhizæ and the tree have a more mutual relationship to each other than that of parasite and host. The fungus obtains its organic substances from the tree whilst the tree is supplied

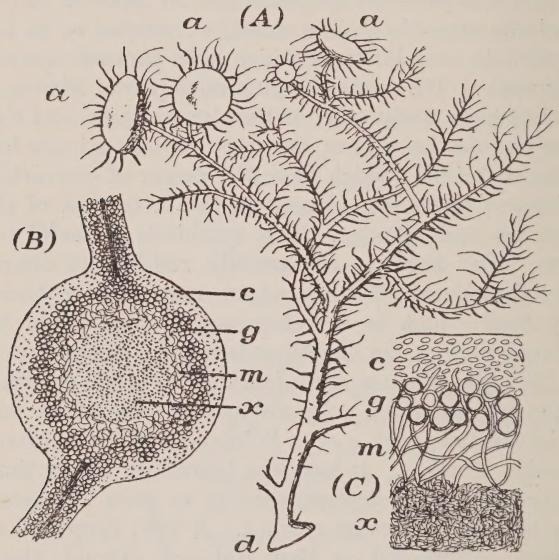

Fig. 122.—Symbioses.

Fruticose lichen (*Usnea florida*). *A*, portion of thallus (× 1½). *B*, T.S. of thallus (× 40). *C*, portion of T.S. of thallus (× 200). *a*, reproductive bodies (apothecia); *c*, cortical region of closely-packed filaments; *d*, attaching disc; *g*, algal (gonidial) layer; *m*, medullary region with loosely-entangled fungal filaments (hyphæ); *x*, axis of crowded hyphæ.

with water and dissolved substances by the fungal filaments, which therefore take on the functions of root-hairs.

Lichens. Another good example of symbiosis is shown by the group of plants known as lichens. These are the non-flowering plants which drape and festoon our trees and rocks with their fronds, threads and incrustations of various hues, shapes and sizes. They have been shown to be com-

pound plants consisting of associated fungi and algæ (Figs. 122 and 221) living together to their mutual benefit. The algal cells benefit from the absorptive powers of the fungal filaments, the fungus is supplied with carbohydrates by the photosynthetic activity of the algal cells, whilst both associates or *symbionts* are able to develop a more complex plant-body and can live in situations which would be fatal to either associate if living alone.

Algæ and Liverwort. Algæ are also able to live in cavities in the tissue of Anthoceros and other liverworts, and, no doubt, both organisms benefit by the symbiosis, though the nature of the benefit is not so evident.

CHAPTER XX

THE CLASSIFICATION OF PLANTS

All of us are more or less familiar with the buttercup which adorns our pastures with its yellow blooms in the summer months. The acrid buttercup has a leaf which is cut up into narrow leaflets, its stem is often over a foot high, its flower stalk is cylindrical and bears yellow flowers and its fruit is a collection of smooth akenes. At first we might think that all the buttercups are of one kind, but careful examination soon reveals to us that there are several kinds of buttercups. In May the predominant buttercup in the pasture is different from the acrid buttercup to which the above description refers. Its leaflets are somewhat broader, its stem is usually less than a foot high, its flower stalk is furrowed and squarish in section, its flowers have reflexed sepals (Fig. 54, *G*) and are of a deeper yellow, and if we dig it up we find that the base of the stem is swollen. This last character causes the dominant May buttercup to be called the bulbous buttercup. On the damper sides of the field a third kind of buttercup may be found, and, as it has a runner which gives off shoots at intervals, it is known as the creeping buttercup (Fig. 54, *A*). Its leaflets are slightly broader than those of the bulbous buttercup and, though it agrees with that in the shape of the flower-stalk, its sepals are not reflexed and there is no bulbous swelling at the base of the stem. Generally its flowers are larger and of a deeper yellow than either of the other buttercups mentioned. The lesser celandine with its broadly cordate or renate leaves (Fig. 31) is also rightly considered to be a kind of buttercup, and if we search a cornfield we should probably find another kind of buttercup which looks different from any

of those we have mentioned, especially in the fruiting stage. The akenes of this corn buttercup, or corn crowfoot as it is more usually called, are ornamented with little spikes. We have not yet noticed all the different kinds of buttercup, as we have one which grows in a wood (wood crowfoot), another which occurs in water and bears white flowers (water crowfoot), another with lanceolate leaves (spearwort) and several others.

Species. All these different kinds of buttercups are placed in the genus *Ranunculus* and each kind is said to be a species. The bulbous buttercup is *Ranunculus bulbosus*, the creeping buttercup is *R. repens*, its specific name indicating its creeping character, the acrid buttercup is *R. acris*, and so on, each kind of *Ranunculus* being distinguished by a specific name which often expresses some particular character it has. The genus *Ranunculus* then includes a number of different species, all of which agree in having both petals and sepals on the flower and in having fruits which are one-seeded akenes.

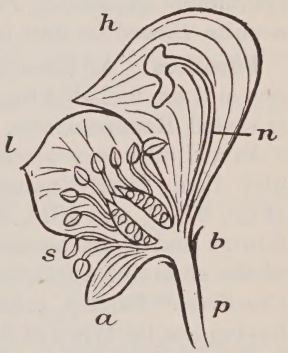

FIG. 123.—Median Vertical Section.

M.V.S. of flower of monkshood (*Aconitum*). *a*, anterior sepal; *l*, lateral sepal; *h*, hood (posterior sepal); *b*, bract; *p*, pedicel; *s*, stamen; *n*, petal modified to serve as a nectary.

Genera. We also know other plants which seem to be nearly akin to *Ranunculus*. The wood anemone looks like a white buttercup, but its petals are absent, the sepals becoming white and petaloid, and there is a whorl of three bracts on the flower-stalk, so it is placed in a separate genus called *Anemone*, our wild wood anemone being *A. nemorosa*, the specific name indicating that it grows in woods. The marsh marigold is separated from the true buttercups and placed in the genus *Caltha* chiefly because its fruits are follicles and not akenes. In *Helleborus* (Christmas rose) the fruit is a follicle and the petals are modified to form nectaries. The globe-flower looks like a double buttercup, but its fruits are follicles and it is

placed in the genus *Trollius*. The common monkshood, which belongs to the genus *Aconitum*, does not at first sight appear to be related to the buttercup. Careful examination, however, shows that its flower (Fig. 123) has five blue sepals, one of which is modified into a large hood, five blue petals, three of which are very small whilst the other two serve as nectaries, a large number of stamens, and three or more follicles, so that in many respects it agrees with the flowers of those we have been considering. Other plants which, on examination and comparison with the buttercup, show kinship, are the columbine (*Aquilegia*, Fig. 82, *A*), peony (*Pæonia*), winter aconite (*Eranthis*) and larkspur (*Delphinium*).

Families. All these plants show a kinship with the buttercup and are included together in the buttercup family, which is styled Ranunculaceæ.

In a similar way we may make other groups of plants and give them family names. The mustard, cress, wallflower (Figs. 67, *C*, and 131), stock and honesty (Fig. 67, *A*) have flowers and fruits possessing similar characters and because of the cross-like appearance of the flower the family is called Cruciferæ. Parsley, celery, carrot, parsnip, etc., all agree in having similar types of flowers arranged in umbels (Fig. 126) and are placed in the family Umbelliferæ. Daisies (Fig. 139), dandelions (Fig. 62), ragworts, asters, sunflowers, thistles and many others have compound flowers of similar structure, and form the family Compositæ. We may proceed in this way to group all our plants into different families and then employ similar methods in grouping the families into orders.

Orders. The water-lily family (Nymphaceæ) and the magnolia family (Magnoliaceæ) agree with Ranunculaceæ in general characters, and especially in having many carpels, so these three families (with some others not mentioned) are placed under the order Polycarpicales.

Classes. The orders containing the flower- and fruit-bearing plants may be grouped in two classes. The class to which most of our flowering plants belong is Dicotyledons, as the seed contains two cotyledons. Grasses, sedges, lilies, orchids, etc., belong to Monocotyledons, the seed possess-

ing one cotyledon only. The usual differences between the two classes is shown below in a tabular form, though many exceptions occur.

TABLE OF DIFFERENCES BETWEEN MONOCOTYLEDONS AND DICOTYLEDONS

	DICOTYLEDON.	MONOCOTYLEDON.
Roots . . .	Tap root often present. Secondary thickening.	Usually adventitious. No secondary thickening.
Bundles .	2–5.	5 or more.
Wood vessels	More or less polygonal in transverse section.	Circular or almost so in transverse section.
Stem . . .	Often well developed.	Often little evident.
Bundles .	Arranged in a ring parallel to periphery.	Scattered in an irregular manner.
	Longitudinal course parallel to periphery.	Run obliquely and longitudinally downwards from centre towards periphery.
Cambium .	Present. Secondary thickening occurs.	Absent. No secondary thickening.
Wood vessels	Usually small.	Usually large.
Leaves. . .	Usually little longer than broad.	Usually much longer than broad.
Venation .	Net.	Parallel.
Bract . . .	Usually similar to leaf or smaller.	Variable but often forms a spathe.
Flower. . .	Parts in twos or fives.	Parts in threes.
	Sepals and petals usually well differentiated.	Sepals and petals alike or similar.
	One sepal usually posterior.	One petal posterior.
Pollen-mother cell	Divides by free-cell method.	Divides in ordinary way.
Embryo . .	General differences occur in its development.	
Seed . . .	Two cotyledons. Often non-endospermic.	One cotyledon. Usually endospermic.
Reserve . .	Usually starch.	Usually sugar.

Exceptional Characters. Among **Dicotyledons** which show characters exceptional to the group, the following examples may be mentioned. The leaves of ribwort plantain (Fig. 39, *A*) and the grass-leaved vetch are long and narrow and the veins are parallel or almost so. The flowers of the dock are trimerous (three parts in each whorl), and its sepals

and petals are so much alike that it may be said to have a perianth of six segments. A transverse section of the white bryony and other members of the cucumber family shows the bundles somewhat irregularly arranged in two rings (Fig. 99, *C*) and the vessels large. In Cyclamen the two cotyledons are so fused together that only one cotyledon appears to be present.

Examples of **Monocotyledons** showing exceptional characters are the following. The leaves of the cuckoo-pint, black bryony and herb Paris are broad and somewhat net-veined, though the venation is of a slightly different type from the net-veining of a dicotyledon. The flowers of herb Paris are usually tetramerous. A kind of secondary thickening occurs in the dragon-tree (*Dracæna*).

Phylum. The big group (phylum) to which these two classes belong comprises all the vascular plants which bear flowers. It is often known as Phanerogamia (see p. 183), but, as the production of seed by these plants is a more critical discrimination from the lower groups of plants than flower-bearing, it is better labelled Spermophyta, which means seed-plants.

Gymnosperms. No mention has been made in the above account of the group of plants to which the pine belongs. In this group the ovule is not enclosed in an ovary and therefore the seed is not in a fruit. To make the classification complete we place the fruit-bearing Dicotyledons and Monocotyledons in the sub-phylum Angiospermæ whilst the naked-seeded conifers and cycads are placed in the sub-phylum Gymnospermæ (see Chap. XXVII). The suffix sperm in each case indicates seed while the prefixes angio- and gymno- respectively indicate clothed and naked.

Systematic Position. As an example of the systematic placing of a plant, the classification of the creeping buttercup is given below.

Species *repens*. Genus *Ranunculus*.

Family *Ranunculaceæ*. Order *Polycarpicales*.

Class *Dicotyledones*, Sub-phylum *Angiospermæ*, Phylum *Spermophyta*.

Phanerogams and Cryptogams. In order to make the account of the classification of plants general, the lower plants must also be considered. The older botanists had the idea that the method of reproduction in the flowering plants was manifest or open whilst that in the non-flowering plants was concealed. They knew that the pollen was brought to the stigma of a flowering plant and that in consequence the ovule was changed into a seed, therefore they called the flowering plants Phanerogamia, a name formed from two Greek words meaning open and union. The non-flowering plants had a concealed or cryptic method of reproduction and so they were labelled Cryptogamia.

Nowadays the use of the microscope has revealed the method of reproduction in most of the cryptogams, and it is more usual to place all plants under four phyla, the flower-producing and seed-bearing plants being called **Spermophyta**, whilst the non-flowering plants form three phyla, **Pteridophyta, Bryophyta** and **Thallophyta.** The ferns, lycopods, horse-tails and club-mosses are vascular plants forming the phylum Pteridophyta ; the mosses and liverworts constitute the phylum Bryophyta, whilst the still lower forms of plant life (algæ, fungi) are placed in the phylum Thallophyta. The distinctions between these lower groups will be considered in more detail later (Chaps. XXVI–XXXI).

Definition of Species. No attempt has been made in the preceding paragraphs to give a rigorous definition of species, genus, family, order, class or phylum ; in fact, it is impossible to do so. Many attempts have been made to give a rigorous definition of a species, but the wide diversity of opinion among systematic botanists as to the naming of plants is sufficient evidence of the failure of these attempts. The same plant may be called by one systematist a species, whereas another systematist considers it to be merely a variety or a form of the species. The term species is then a convenient name for an assemblage of interbreeding individuals, varying among themselves, but sufficiently alike to be called by the same name. These individuals under natural conditions preserve their general resemblances to one another and do

not depart far from the type or average individual. By selecting and cultivating under suitable conditions a slight variation from the type, a large number of individuals, showing that variation, may be formed and reproduced, but this smaller assemblage is not a species and is often termed a race or strain.

CHAPTER XXI

SOME OF THE CHIEF FAMILIES OF FLOWERING PLANTS

During the consideration of the families of flowering plants, some typical member of each family should be examined carefully, drawn and described. For example, the buttercup can be taken as a type of Ranunculaceæ, the white dead-nettle for Labiatæ and the bluebell for Liliaceæ. Afterwards, as many plants as are available should be examined, especially in regard to similarities to and differences from the typical plant. The different parts of the plants should be taken in order, and an attempt made to find out the characters in which the various plants agree. Thus, in the family Ranunculaceæ, we may be able to examine several species of buttercups together with anemones, columbines and monkshood. Neither the roots nor the stems show any strongly marked agreement. The leaves are, in most cases, markedly lobed in a palmate manner, and this may be considered to be a general character of the family, though exceptions (e.g. lesser celandine) may occur. Again, the flowers are perfect and regular (except the monkshood), and these characters may be considered general for the family. The fruit in all our examples is either an akene or a follicle, so that we may put down "fruit, an akene or follicle" as a family character. In this way, root, stem, leaf, inflorescence, bract, flower, calyx, corolla, andrecium, gynecium, fruit and seed may be considered, and a list of general characters of the family made out.

Floral Formula. It is useful to use a floral formula in order to express in a brief and concise manner the number of petals, sepals, stamens and carpels and their relationships.

The floral formula of the buttercup is K 5 C 5 A ∞ G $\underline{\infty}$ where K 5 indicates that the calyx is polysepalous and has 5 sepals, C 5 that the corolla is polypetalous and consists of 5 petals, A ∞ that the stamens are many (usually more than 20), and G $\underline{\infty}$ that the gynecium is apocarpous and has numerous carpels, the line beneath indicating that the carpels are placed above the rest of the floral parts. When the flower is epigynous, the line is placed above the numeral denoting the number of carpels. When the numbers are in brackets, cohesion between the parts is indicated, thus K (5) means that the 5 sepals are joined together. A line above and between two of the symbolic letters denotes adhesion between the parts represented, thus C $\overbrace{(5)\ A}$ 5 means that the stamens are fixed on the 5-partite gamopetalous corolla. The snapdragon has a hypogynous flower with a gamosepalous calyx of 5 sepals, a gamopetalous corolla of 5 petals, an andrecium of 4 epipetalous stamens and a gynecium of 2 syncarpous carpels. Its floral formula is therefore K (5) C $\overbrace{(5)\ A}$ 4 G (2). Two other symbols are sometimes used to denote the symmetry of the flower.

Symmetry of Flower. When the flower can be divided into similar halves by means of any diameter, it is said to be regular or **actinomorphic**, and this is shown by the symbol $\oplus$. When the floral parts are of different shapes or sizes so that the flowers cannot be divided into two similar halves by any diameter, it is said to be irregular. Most irregular flowers can be divided into two similar halves along one plane, and they are then said to be **zygomorphic.** To denote the zygomorphic condition an arrow is used, the direction of the arrow representing the diameter along which division into two halves occurs. A few flowers are so irregular that they cannot be divided into similar halves along any diameter, and they are then said to be **asymmetric.** When these symbols are used, the floral formula of the buttercup is $\oplus$ K 5 C 5 A ∞ G $\underline{\infty}$, whilst that of the snapdragon is $\downarrow$ K (5) C $\overbrace{(5)\ A}$ 4 G $\underline{(2)}$.

Floral Diagram. A floral diagram is a useful way by which the relationships of the various parts of the flower to each other and to the inflorescence axis can be shown. It is a kind of ground plan of the flower with the axis behind (at the top of the diagram) and the bract in front. Fig. 124 represents the floral diagram of the snapdragon. The flower stands in the axil of the bract, so that *a* represents the inflorescence axis, and *b* the bract. A sepal is represented by *s*, a petal by *p*, and cohesion is indicated by connecting lines. A stamen is represented by *st*, the connecting line indicates that it is epipetalous, and the small dip that it splits towards the inside of the flower. The dot represents

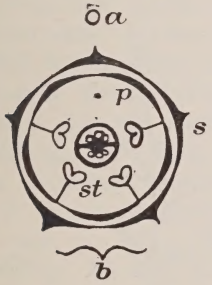

FIG. 124.—Floral Diagram of Snapdragon.

a, position of inflorescence axis; *b*, bract; *s*, sepal; *p*, petal; *st*, stamen.

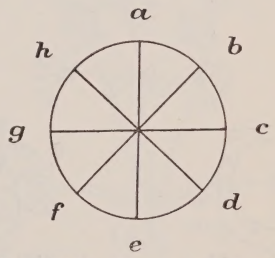

FIG. 125.—Planes of Symmetry in a Flower.

ae, antero-posterior or median; *cg*, lateral; *bf* and *dh*, diagonal planes.

the missing posterior stamen. The central part of the diagram is practically a cross-section of the ovary, and shows that there are two median carpels joined together, and that the placentation is axile. The chief difficulty experienced in making floral diagrams is that of deciding which is the posterior and which the anterior portion of the flower. It is usually easy to do this when the flower is zygomorphic, but, when the flower is regular, it is often difficult to do so, and seems to be unimportant. When a bract is present it denotes the anterior portion and in most dicotyledons (Papilionaceæ are exceptional) one sepal is posterior. Fig. 125 shows the

planes of a flower or of a floral diagram. The plane *ae* is the antero-posterior or median, *cg* is the lateral and *dh* and *bf* are diagonal planes.

The manner in which the sepals or petals fit with each other is sometimes shown in the floral diagram, and the relative sizes of the petals may be indicated. By the use of coloured crayons, the colours of the different parts may be represented. Such methods tend to make the floral diagram too complicated, and are seldom, if ever, used in the diagrams shown in this chapter.

Inflorescences. The two main kinds of inflorescences are racemose and cymose. In a racemose (indefinite or

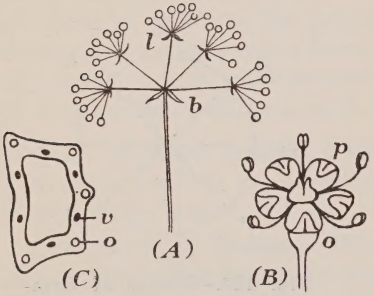

FIG. 126.—Compound Umbel.

A, diagram indicating bracts (*b*) and bracteoles (*l*). *B*, flower of fennel: two stigmas are shown in the centre and an epigynous honey-disc surrounds their bases: *o*, inferior ovary; *p*, incurved petal. *C*, T.S. of fruitlet (mericarp) of fennel: *o*, oil canal; *v*, vascular bundle.

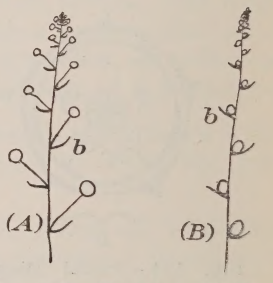

FIG. 127.—Diagrams of Raceme (*A*) and Spike (*B*).

The circles represent flowers and the lines below them bracts.

centripetal) inflorescence the flowers are borne on branches from the main axis, whilst in a cymose (definite or centrifugal) inflorescence, the axis terminates in a flower, the inflorescence axis being continued by a branch. When the flower arises in the axil of a bract, the inflorescence must be racemose, and the youngest flowers are towards the centre of the inflorescence. When the pedicel is opposite the bract, or the central flower of the inflorescence is the first to open, the inflorescence is a cymose one. Racemose branching in an inflorescence there-

fore corresponds to what was described as monopodial for a stem (see pp. 37, 38 and 42), whilst cymose corresponds to sympodial.

The chief kinds of **racemose** inflorescences are : (*a*) the raceme (Fig. 127, *A*) with an elongated axis (peduncle) and each flower having a stalk or pedicel ; (*b*) the corymb (Fig. 90) which only differs from an ordinary raceme in having the flowers almost at the same level, owing to the lengthening of the pedicels of the outer flowers (see p. 124) ; (*c*) the spike (Fig. 127, *B*) in which the flowers are sessile on an elongated axis ; (*d*) the spadix (Fig. 87), which is like a spike but has a fleshy axis (see p. 121) ; (*e*) the capitulum (Figs. 62 and 139), with sessile flowers crowded together on an axis which is short and broad (see p. 82) ; (*f*) the umbel (Figs. 89 and 126), in which the upward growth of the axis is arrested and the pedicels of all the flowers arise at the same level (see p. 124).

FIG. 128.—Dichasium of Greater Stitchwort.

The flowers are numbered in order of development ; 1, withered flower ; 2, open flower ; 2′, flower just open ; 3, 3′ and 4, flower buds just beginning to open ; *b*, bracts.

The chief forms of **cymose** inflorescence are : (*a*) the cyme or *monochasium* with single flowers arising at different levels on the false axis (sympodium), e.g. forget-me-not ; (*b*) the *dichasium* with the main axis terminating in a flower, whilst two branches form daughter axes in which the process is repeated, e.g. stitchwort (Fig. 128) ; (*c*) the *pleiochasium*, in which the main axis terminates in a flower, whilst three or more daughter axes are formed below. This is similar to an umbel, but differs in that the first flower to open is the central

one. It is sometimes called a cymose umbel and is shown in the elder.

A few other terms are in general use. **False dichotomy** is often used instead of dichasium. A **catkin** or **amentum** (e.g. hazel, Fig. 84) is a peculiar form of deciduous spike in which the flowers are unisexual and have the corollas absent or reduced, protection being afforded by bracts and bracteoles. A **panicle** is strictly applied to a much branched raceme, but is sometimes used for a pyramidal kind of inflorescence in which the secondary branching is cymose. Many inflorescences are of a **mixed** character. The general branching may be racemose, whilst the smaller groups of flowers are formed in a cymose manner. Such a raceme of cymes is shown in *Calceolaria*. Other compound inflorescences as a raceme of capitula, a raceme of spikes, etc., are sometimes found.

DICOTYLEDONS

Ranunculaceæ

Characters. Herbs (clematis is woody), often poisonous (especially aconite), annual or perennating by rhizomes (anemone), runners (creeping buttercup) or tuberous roots (lesser celandine, Fig. 31). *Leaves alternate* (opposite in clematis), mostly radical, usually *exstipulate*, amplexicaul (sheathing at the base), *much-divided* (linear in mousetail, lanceolate in spearwort, cordate to renate in lesser celandine (Fig. 31), renate in marsh marigold), and without oil glands. *Inflorescence usually cymose* (racemes in monkshood and larkspur). *Flower perfect* (Fig. 54), *hypogynous, polypetalous, usually regular*; zygomorphic in monkshood (Fig. 123) and larkspur. Petals often absent or reduced to nectaries. In anemone, marsh marigold and clematis, the coloured portion of the outer floral envelope is usually regarded as a petaloid calyx. In hellebore and monkshood (Fig. 123) the nectaries are usually regarded as modified petals. *Stamens indefinite with anthers splitting towards the outside of the flower* (extrorse). *Pistil apocarpous, usually of many carpels and with anatropous ovules. Fruit* (Figs. 54, 67, 69) *usually a collection of akenes or follicles* (berry in baneberry). Seed non-endospermic.

Floral Formula. The typical one is that of the buttercup, K 5 C 5 A ∞ G $\underline{\infty}$. Examples of other floral formulas are: lesser celandine, K 3 – 5 C 7 – 12 A ∞ G $\underline{\infty}$; anemone and marsh-marigold, K 5 – 9 C 0 A $\underline{\infty}$ G $\underline{\infty}$; columbine, K 5 C 5 A ∞ G $\overline{5}$; clematis and meadow-rue, K 4 – 5 C 0 A ∞ G $\underline{\infty}$; monkshood ↯ K 5 C 2 – 5 A ∞ G $\underline{3 - 5}$.

Pollination is chiefly by means of insects. The flowers are open and other methods may occasionally occur; also self-pollination easily occurs. The bright flowers and the presence of nectaries (Fig. 54) indicate insect-pollination. Honey-spurs are present in columbine, larkspur and monkshood.

British Plants. Buttercups, crowfoots, lesser celandine, spearwort, clematis (Fig. 51), mousetail (Fig. 170) columbine (Fig. 82), meadow-rue, hellebore, globe-flower, marsh marigold, anemone, monkshood (Fig. 123), larkspur, peony.

Cultivated Plants. Christmas rose, *Nigella* (with capsule), etc.

Cruciferæ

Characters. Herbs with alternate and exstipulate leaves. Inflorescence usually an *ebracteate* (i.e. without bracts), raceme

Fig. 129.—Floral Diagram of Cruciferæ.

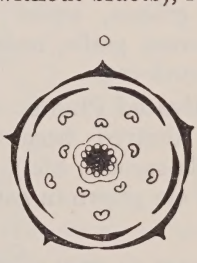

Fig. 130.—Fl. D. of Caryophyllaceæ. (*Lychnis.*)

or *corymb*. *Flower* (Figs. 129 and 131) *perfect, hypogynous, polypetalous, usually regular* (petals unequal in candytuft). Corolla with *four petals*, arranged like a Maltese cross (*cruciform*) on the diagonal planes. *Stamens six*, in two whorls, the two outer and lateral short, and the four inner long (*tetradynamous*). The four inner stamens appear to

have been produced by the branching or splitting (chorisis) of the posterior and anterior stamens. *Fruit* (Fig. 67) *a siliqua or silicula with a false partition* (*replum*). *Ovules numerous on a parietal placenta.* Seeds non-endospermic.

Floral Formula. K 2 + 2 C × 4 A 2 + 2^2 G $\underline{(2)}$. The × indicates that the petals are in the diagonal planes, and the 2^2 denotes that the four inner stamens have been derived from the splitting of the original two inner stamens.

Pollination. Nectaries are present as small green bodies at the bases of the short stamens (Fig. 131), and the flowers are arranged in conspicuous corymbs. Insect pollination is therefore suggested, but the flowers are fairly open ones and the flower is often only slightly protandrous, so that pollination may be effected by other means and self-pollination may easily occur. The sepals are often somewhat erect and the lateral ones are larger and imbricated with the outer ones so that honey cannot be easily obtained from the base of the flower.

British Plants. Wallflower (Fig. 131), mustards, cresses, radish (fruit a jointed pod), stock, rockets, shepherd's purse, whitlow-grass, sea-kale, woad (fruit an indehiscent pod), scurvy-grasses, sweet alyssum, candytuft, cuckoo-flower, water-cress, garlic, mustard, charlock, wild cabbage, penny-cress, rock-cress.

Cultivated Plants. Honesty (Fig. 67), turnip and many plants derived from the cabbage (cauliflower, broccoli, Brussels sprouts, etc.), as well as some of those mentioned above, are grown in gardens.

Caryophyllaceæ

Characters. Herbs with *swollen nodes. Leaves opposite*, decussate, usually entire and exstipulate. Inflorescence cymose, often a *dichasium* or false dichotomy (Fig. 128). *Flowers* (Figs. 130 and 132) *regular, polypetalous*, hypogynous (somewhat perigynous in some cases), usually perfect, pentamerous (parts in fives) and complete. The petals (Fig. 132) often have a narrow basal portion (claw) and an expanded upper part (limb). A little outgrowth called a ligule (Fig. 132, *l*)

is sometimes present at the junction of the claw and limb (e.g. campion). *Stamens definite, usually twice as many as the sepals or petals.* Anthers splitting towards the inside of the flower (introrse). *Pistil of* 2–5 *carpels, syncarpous*;

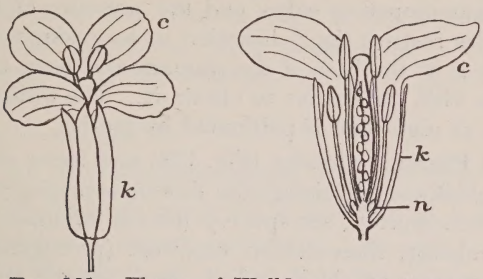

FIG. 131.—Flower of Wallflower and M.V.S.

The length of the thalamus is slightly exaggerated. Two small nectaries (*n*) are at the bases of the short stamens. *k*, sepal; *c*, petal.

styles free; ovary one-chambered, each chamber or loculus containing many ovules on a *free-central placenta*. Fruit usually a *one-chambered* (*unilocular*) *capsule* with either apical teeth (Fig. 71) or valves. Seeds with perisperm and curved embryo; censer mechanism is often responsible for their dispersion.

The family may be divided into two groups or tribes:—(1) Alsinoideæ, the chickweed tribe, in which the calyx is polysepalous (Fig. 128); (2) Silenoideæ, the campion tribe, in which the calyx is gamosepalous (Fig. 132).

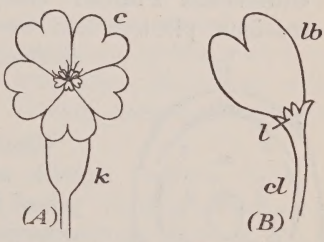

FIG. 132.—Campion (*Lychnis*)

A, pistillate flower. *B*, single petal; *k*, tube of gamosepalous calyx; *c*, petal; *cl*, claw; *lb*, limb; *l*, ligule.

Floral Formula. K 5 C 5 A 5 + 5 G $\underline{(2-5)}$ is typical of the Alsinoideæ. K (5) C 5 A 5 + 5 G $\underline{(2-5)}$ is a general one for the Silenoideæ. A vertical line is sometimes placed between the C 5 and the A to indicate that the outer whorl of stamens is opposite to the petals.

Pollination. Insect pollination is the rule. In the chickweed tribe the flowers are open ones and pollination can be performed by short-tongued insects. Protandry is very slight and self-pollination often occurs. In the campion tribe the gamosepalous calyx and the presence of ligules in some species restrict the pollination to long-tongued insects. The honey is at the base of the stamens and bees, butterflies and moths visit the flowers to obtain it. The white campion is odorous at night and is pollinated by moths.

British Plants. Greater (Fig. 128) and lesser stitchwort, common chickweed (cleistogamic flowers sometimes occur in winter), corn-spurrey, sea-spurrey (leaves stipulate), thyme-leaved sandwort, three-nerved sandwort (protogynous), sea-purslane, mouse-ear chickweed (in some species petals may be absent ; in one species which is frequent on sand-hills, the flower is tetramerous), pearlworts (both apetalous and tetramerous species occur), red (Fig. 132) and white campions (dicœcious), ragged robin, corn-cockle, bladder-campion, sea-campion, soapwort, pinks and the so-called catchflies.

Cultivated Plants. Many species of *Dianthus* (pinks, carnations, picotees and Sweet William) are cultivated for their odorous flowers.

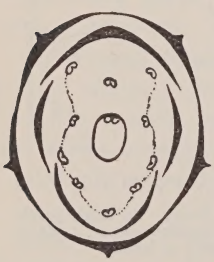

Fig. 133.—Fl. D. of Papilionaceæ illustrating Zygomorphy and Diadelphy.

Papilionaceæ

Characters. Herbs, shrubs or trees with *alternate, stipulate, usually compound leaves. Roots with tubercules for absorption* of nitrogen (see p. 175). *Inflorescence racemose. Flowers* (Figs. 55 and 133) *irregular, perfect,* slightly perigynous, *polypetalous. Corolla papilionaceous* (butterfly-shaped, consisting of a posterior standard, two lateral wings, and two anterior petals somewhat joined together to form the keel). *Stamens ten, monadelphous* (broom, furze, dyer's greenwood, rest-harrow), *or diadelphous* (peas, vetches, medick, trefoils). *Pistil* (Fig. 56) *of one carpel* with ovules on a

parietal placenta. *Fruit a legume* or lomentum (a kind of legume with transverse septa). Many of the plants show modifications for climbing purposes. The stems twine in the kidney bean (Fig. 28). Many vetches have some or all the leaflets changed into tendrils (Figs. 48–50), compensation for the loss of leaf-surface being afforded by a winged stem (sweet pea) or by the enlargement of the stipules (vetches, see p. 66).

Floral Formula.

In the monadelphous species K (5) C 5 A (5 + 5) G 1.

In the diadelphous species K (5) C 5 A (5 + 4) + 1 G 1.

Pollination. Insect pollination general. The insect alights on the wings, its weight depresses them and the keel which articulates with them, and the essential organs are liberated.

British Plants. Dyer's greenweed, rest-harrow, melilot, kidney-vetch, bird's-foot trefoil. Petty whin, gorse (Fig. 52), and spiny rest-harrow with stem-spines. Broom has its leaves reduced to scales and is a good example of a switch plant. Medick (Fig. 41) has its flowers usually crowded and its fruits coiled and indehiscent. Clovers and trefoils with flowers in racemose heads and leaves trifoliate. Bird's-foot with a lomentaceous (jointed) fruit. Vetches, tares and everlasting pea usually with tendrils.

Cultivated Plants. *Genista*, *Galega*, *Lupinus*, *Laburnum* and *Wistaria* are ornamental plants. *Robinia pseudacacia* is the false acacia, and its stipule spines are shown in Fig. 41. The seeds of *Pisum* (pea), *Lens* (lentil), *Faba* (bean) and *Phaseolus* (kidney-bean) are used as food.

Allied Families. Papilionaceæ belongs to the order Leguminosæ, and is the only family of Leguminosæ which has British representatives. The families Mimosaceæ and Cæsalpiniaceæ have flowers which are not papilionaceous, but as they agree with Papilionaceæ in the character of the pistil and fruit, they are placed in the same order. The true Acacias and *Mimosa* belong to the former, whilst the ornamental plant *Gleditschia* is a member of Cæsalpiniaceæ.

Mimosa pudica is the sensitive plant which responds so readily to a contact stimulus. On nipping a terminal leaflet, the lower leaflets fold over and if the stimulus is strong enough all the leaflets of the plant will close and the folded leaves droop towards the stem. The acacias are often provided with stipule spines (Fig. 30), which provide both home and food for ants. The leaf stalk in many acacias becomes broadened out and forms a leaf-like body (phyllode).

Rosaceæ

Characters. Trees, shrubs, or herbs with *alternate*, usually *stipulate* and *often compound leaves*. The herbaceous plants perennate by means of runners (cinquefoil, strawberry, Fig. 27), stolons (bramble, Fig. 27), or suckers (raspberry). Parsley-piert is annual. Inflorescence racemose (Fig. 50) or cymose, chiefly the latter. *Flowers* (Fig. 134) *regular, perfect* (salad burnet is moncœcious), *polypetalous, perigynous*. The perigyny is slight in some (bramble) and almost merges into epigyny in others (rose, apple). Calyx is sometimes gamosepalous and an epicalyx (Fig. 134) is occasionally present. The corolla is usually conspicuous, but is absent in salad burnet, great burnet and lady's mantle. *Stamens usually numerous* and apparently inserted on the sepals or on a disc from which the free parts of the sepals come off. *Pistil apocarpous*, often with many carpels. Fruit (Figs. 65–66, and 68, *C*) variable. The perigyny of the flower and stipulate character of the leaf are the chief distinctions from Ranunculaceæ.

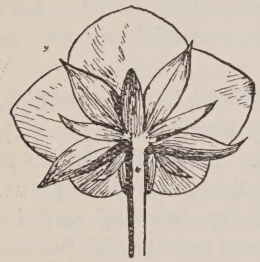

Fig. 134.—Strawberry.

Flower viewed from below, so as to show the epicalyx which appears like an outer whorl of small sepals.

Floral Formula. General: K 5 C 5 A 2 – ∞ G 1 – ∞.

Typical: K 5 C 5 A ∞ G ∞.

Meadow-sweet, K (5) C 5 A 5 + 5 G 5.

Agrimony, K (5) C 5 A 5 + 5 + ⁞ G 2.

Pollination. Except in the salad burnet pollination is effected by means of insects. The flowers are usually showy, often odorous, and honey is secreted on the inner surface of the usually concave receptacle.

British Plants. These are grouped into tribes chiefly by the kind of fruit borne. In avens (Fig. 68, *C*), cinquefoil, tormentil, silverweed, lady's-mantle, parsley-piert, agrimony, salad burnet and great burnet, the fruit is an akene. The meadow-sweet has a few-seeded follicle. The sloe, plum and cherry have drupes. In the blackberry (Fig. 65) and raspberry the drupes are small and clustered. In the strawberry the thalamus becomes juicy, the true fruits being akenes. The rose (Fig. 65), apple (Fig. 66), pear, mountain ash, white beam and hawthorn have their carpels enclosed by the upward growth of the receptacle.

Cultivated Plants. Many species of the above are grown for their flowers or fruits. The cherry-laurel, peach, apricot, almond, loganberry, cotoneaster, medlar and quince also belong to this family.

Umbelliferæ

Characters. Chiefly North Temperate herbs or shrubs with *fistular* (hollow) *stems and alternate, exstipulate, amplexicaul* (sheathing at the base, Fig. 33), usually large and *much-divided leaves.* Root often a long tap-root (carrot, Fig. 12). *Inflorescence an umbel,* usually a compound one with bracts and bracteoles. *Flowers regular* (Figs. 126 and 135), but frequently somewhat irregular owing to the enlargement of the outermost petals, perfect, *polypetalous, epigynous, pentamerous.* Calyx rudimentary or absent. *Stamens five,* introrse. *Pistil bicarpellary, syncarpous* ; stigma bilobed, the base of the two styles being fleshy and thickened to form an epigynous honey-disc ; ovary bilocular with a suspended ovule in each loculus. *Fruit a schizocarp* (Fig. 72, *B*) *dehiscing into two fruitlets* (*mericarps*). Each mericarp is

Fig. 135.—Fl. D. of Umbelliferæ.

often marked by ridges with intervening oil-ducts (Fig. 126). Seed endospermic.

Floral Formula. K 0 – 5 C 5 A 5 G $\overline{(2)}$.

Pollination. The aggregation of the small flowers into umbels, the aromatic oils present in all parts of the plant, the marked protandry and the epigynous honey-disc of the flowers indicate that cross pollination by means of insect visitors is the regular method. Flies are the chief insect visitors.

British Plants. Marsh-pennywort (simple orbicular leaves and simple umbel), sea-holly (leaves prickly ; flowers in compact cymose heads), wood-sanicle, hemlock (very poisonous), alexanders, hare's-ear (simple leaves), wild celery (very poisonous), marshwort, water-parsnip, stone-parsley, cowbane (very poisonous), wild parsley, goutweed, cow-parsnip (Fig. 33), hedge-parsley, chervil, samphire (leaves fleshy), burnet-saxifrage, fool's-parsley (very poisonous), wild carrot, wild parsnip, dropwort, angelica, shepherd's-needle (fruits very long), fennel (Figs. 72, *B*, and 126).

Cultivated Plants. Parsley, carrot (Fig. 12), parsnip, celery, caraway, anise, dill.

Allied Families. The ivy and dogwood belong to families which are akin to Umbelliferæ. The members of Onagraceæ, the willow-herb family (Fig. 74), like umbelliferous plants, have polypetalous, regular and epigynous flowers, but they are tetramerous, the inflorescence is not an umbel and the fruit is a capsule.

Primulaceæ

Primulaceæ is one of the simplest families of the group (Gamopetalæ) in which the petals are joined together.

Characters. Herbs perennating by means of rhizomes (primrose), tubers (cyclamen), etc. Leaves exstipulate, often radical and usually simple (much-divided in the submerged water-violet). Inflorescence often racemose ; an umbel in the cowslip ; a solitary flower in the primrose. *Flowers* (Figs. 85 and 136) *regular*, perfect, *gamopetalous* (almost polypetalous in the pimpernels), pentamerous (occasionally

tetramerous), *hypogynous*, sometimes heterostyled (primrose and cowslip, see p. 119). *Stamens epipetalous, antipetalous* (opposite the petals), introrse. *Pistil of five carpels, syncarpous*; stigma capitate (pin-headed); style single, ovary unilocular; *placentation free-central* (Fig. 116); ovules numerous. Fruit a capsule opening by apical teeth or by a lid (scarlet pimpernel). Seed endospermic.

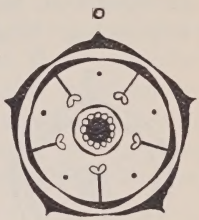

Fig. 136.—Fl. D. of Primulaceæ.

Floral Formula. K (5) C (5) A 0 + 5 G (5). The antipetalous stamens are explained by the suppression of a whorl of stamens. In brookweed and the snow-plant (*Soldanella*) of the Alps, the outer whorl is represented by barren stamens (staminodes). The five carpels are often indicated by the presence of lines on the capsule and by the 5-valved dehiscence of the fruit.

Pollination by means of insects; those with a long tubular corolla by butterflies and bees; those with open flowers by flies. The flowers are often only slightly protandrous and self-pollination is probably frequent. Heterostyly (Fig. 85) occurs in the primrose, oxlip, cowslip and water-violet.

British Plants. Primrose (Fig. 85), cowslip, oxlip, yellow-pimpernel, yellow-loosestrife, moneywort, scarlet-pimpernel, bog-pimpernel, water-violet, brookweed, sea-milkwort (corolla absent).

Cultivated Plants. Many species of *Primula* are grown in gardens and greenhouses. The cyclamen is a favourite pot-plant.

Labiatæ

Characters. Herbs or undershrubs with *quadrangular stems* and *simple, exstipulate, opposite and decussate leaves* (Fig. 47); usually perennating by means of suckers (Fig. 27). The leaves and stems are usually hairy and epidermal glands, containing volatile and aromatic oils, are often present (mints, thyme, lavender, rosemary, etc.). Inflorescence primarily

racemose, but the *small inflorescences are cymose* whorls in the axils of bracts. *Flowers* (Figs. 137, 138) *irregular, perfect, gamopetalous, hypogynous.* Calyx persistent, gamosepalous, tubular or bilabiate (two-lipped). *Corolla bilabiate* with imbricate prefloration (arrangement of the floral leaves when young). *Stamens* four, *didynamous* (two long and two short) and *epipetalous.* The posterior and fifth stamen is suppressed, its position being occupied by the style. *Pistil bicarpellary, syncarpous*; stigma bifid; style reaching to the base of the ovary (*gynobasic*, Fig. 138); *ovary quadrilocular* (four-chambered) owing to the development of a median false septum; placentation axile with one anatropous ovule in each loculus. *Fruit a schizocarp of four nutlets.* Seed non-endospermic.

FIG. 137.—Fl. D. of Labiatæ.

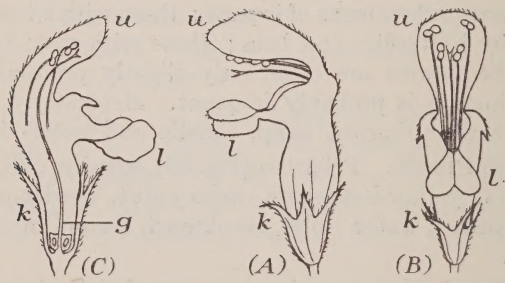

FIG. 138.—Flower of White Dead-nettle.

A, side view. *B*, front view. *C*, M.V.S. *g*, gynobasic style passing down to the base of the ovary; *k*, gamosepalous calyx; *l*, lower lip of corolla; *u*, upper lip.

Floral Formula. ↓ K (5) C $\overbrace{(5)\ A\ 4}$ G (2). Sage (*Salvia*) ↓ K (5) C $\overbrace{(5)\ A\ 2}$ G (2).

Pollination. Cross pollination by means of bees and other insects is general, but self-pollination may occur. The general method is described for the dead-nettle (Fig. 138), and the exceptional method for the sage (Fig. 86) on p. 120. A honey disc is present at the base of the ovary, the flowers

are usually protandrous and the ripe stigmas protrude beyond the stamens. In the ground ivy and some other members of the family flowers, which are pistillate only, sometimes occur.

British Plants. Mints (flowers almost regular and stamens almost equal), thymes, marjoram, gipsywort (two posterior stamens imperfect), wild basil, calamint, balm, horehounds, sage (two stamens and special pollination mechanism, Fig. 86), ground ivy, self-heal, skullcaps, wood-betony, woundworts, germanders, bugle (long runners), hemp-nettles, dead-nettles (Figs. 47 and 138).

Cultivated Plants. Lavender, rosemary (two stamens), hyssop, sweet basil and some species of thyme, sage, mint, etc., are grown in gardens or greenhouses for their showy flowers or for their aromatic oils. Patchouli is exported from Penang.

Scrophulariaceæ

Characters. Herbs or shrubs (many cultivated Veronicas) with *cylindrical* or angular stems and *simple, exstipulate, alternate* or opposite *leaves*. Inflorescence varied, but *not in whorls* as in Labiatæ. *Flowers* (Figs. 57 and 124) *irregular, perfect, gamopetalous, hypogynous*, pentamerous but often modified. Calyx gamosepalous, persistent. Corolla bilabiate, *often personate* (face-like). In the mulleins and speedwells it is almost regular, in the foxglove it is glove-shaped, in the toadflax it is spurred, and in the calceolaria it is slipper-shaped. Stamens five, usually with the posterior stamen suppressed, *didynamous, epipetalous*. *Pistil bicarpellary, syncarpous* ; stigma bifid ; *style terminal* (at the top of the ovary) ; ovary bilocular (two-chambered) ; placentation axile with many anatropous ovules. *Fruit a capsule* with endospermic seeds.

Floral Formula. General : $\downarrow$ K (5) C $\overbrace{(5)\ A\ 4}$ G $\underline{(2)}$.

Mullein : $\downarrow$ K (5) C $\overbrace{(5)\ A\ 5}$ G $\underline{(2)}$. Speedwell (*Veronica*) :

$\downarrow$ K (4) C $\overbrace{(4)\ A\ 2}$ G $\underline{(2)}$.

Pollination. A honey disc is present at the base of the ovary, the flowers are usually somewhat protandrous and the

ripe stigmas protrude beyond the stamens. The open flowers of the mulleins and speedwells are mostly pollinated by flies. Figwort is visited by wasps. In the flowers with longer corolla-tubes (Fig. 57) the insect visitors must have long "tongues" to reach the honey, and various contrivances forcing them to take definite paths are often adopted.

British Plants. Snapdragon (see p. 74), figwort (posterior stamen modified to a scale), mulleins (flowers almost regular and having five stamens with hairy filaments), speedwells and brooklime (flowers almost regular; two stamens), toadflaxes, foxglove and monkey-musk. Toothwort is a parasite on the roots of hazel and other trees. Eyebrights, cowwheats, bartsias, yellow rattles and louseworts are semiparasitic on the roots of grasses and other surrounding vegetation.

Cultivated Plants. Various kinds of *Veronica*, *Antirrhinum* (Fig. 57), *Calceolaria* and *Penstemon* (the posterior and fifth stamen is barren). *Gratiola* has two stamens only.

Allied Families. Scrophulariaceæ is closely allied to the potato and nightshade family (Solanaceæ) in which the flowers are usually regular, the stamens five and the septum between the two carpels placed diagonally instead of being medianly placed, as in Scrophulariaceæ. Labiatæ differ from Scrophulariaceæ in the general arrangement of the flowers and especially in the gynobasic style and schizocarpic fruit. Boraginaceæ is similar to Labiatæ in regard to the four nutlets and the position of the style, but the flowers are usually regular and are not arranged in whorls. Borage, comfrey, forget-me-not, alkanet, lungwort and bugloss are familiar members of this family. The four families are sometimes grouped into the order Tubifloræ, but it is preferable to segregate Solanaceæ and Scrophulariaceæ and put them into a separate order (Personatæ).

Compositæ

This family is the largest and most widely distributed one in the world. It contains over 10,000 species and shows great variety in its vegetative organs. The dandelion is a typical

member of the family, and has been described in Chapter IX. The great success of this family in competition with other families is due to the economy displayed by having a large number of flowers aggregated together, by its method of pollen presentation, by the difficulties which insects experience in obtaining honey without doing some service to the plant, and by the efficient methods of seed dispersal.

Characters. Annual or perennial herbs (some foreign members shrubby), with leaves which are *usually exstipulate*

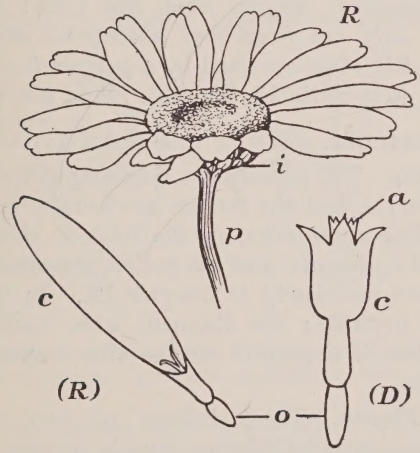

FIG. 139.—Capitulum of Marguerite.

R, ray-floret (× 3). *D*, disc-floret (× 6). *i*, involucre of bracts; *p*, peduncle; *o*, ovary; *c*, gamopetalous corolla; *a*, apices of syngenesious anthers.

and alternate (opposite in sunflower, artichoke, etc.). A tap root is often present and this, and other underground parts, *often contain inulin*. The aerial parts often have *laticiferous vessels* and *oil ducts* are common. Inflorescence a *capitulum* (Figs. 62 and 139) of many small flowers protected by an *involucre of bracts*. The outer florets open first so that the capitulum is centripetal (racemose). Flowers (Figs. 62 and 139) regular or irregular, perfect or imperfect, *gamopetalous* and *epigynous*. In the dandelion all the florets are strap-

shaped or ligulate ; in the daisy the outer florets are ligulate and form a ray round the disc of inner tubular florets ; in the groundsel all the florets are tubular. The ray florets are neuter (without stamens or pistil) or unisexual ; in most cases they are pistillate. The disc florets are usually perfect, but are sometimes unisexual, e.g. in the coltsfoot they are staminate. Scale-like bracts are sometimes present between the florets (cat's-ear, stinking mayweed). *Calyx absent* or reduced to scales or *modified to form a pappus* (Figs. 62 and 64). *Stamens five, epipetalous, syngenesious,* introrse. *Pistil bicarpellary, syncarpous* ; stigma when ripe bifid ; style single ; ovary with only *one basal and anatropous ovule. Fruit a cypsela* (Fig. 64), often crowned by a pappus (e.g. dandelion), or by spines (bur-marigold, Fig. 73). Seed non-endospermic.

Floral Formula. K 0 or modified C $\overbrace{(5)}$ A $\overbrace{(5)}$ G $\overline{(2)}$.

Pollination. The nectary is a ring-shaped body round the base of the style, and the flowers are usually markedly protandrous. The aggregation of the flowers, their protection from marauding insects, and the pollen-presentation mechanism have been mentioned in Chapter IX. In *Centaurea* the stamens are irritable ; the filaments when touched contract and the pollen is deposited on the club-shaped top of the unripe stigma.

British Plants. These belong to two sub-families : (1) Ligulifloræ with laticiferous vessels present and all the florets ligulate. Dandelion (Figs. 62–64), chicory, hawkweed, hawkbit, hawk's-beard, cat's-ear (scaly bracts on receptacle), goat's-beard, sow-thistle, nipplewort (pappus absent), wall-lettuce.

(2) Tubulifloræ with no latex and some or all the flowers tubular. Ray florets are present in aster, daisy, golden rod, ploughman's spikenard, marguerite (Fig. 139), fleabane, camomile, tansy, yarrow, sneezewort, mayweed, ragwort, feverfew, coltsfoot. Tubular flowers only are present in the thistles, cudweeds, burdocks, mugwort, wormwood, hemp-agrimony, saw-wort, groundsel, butterbur, hardheads and knapweeds.

Cultivated Plants. Artichoke is grown for its tubers (Fig. 23) and lettuce for its leaves. Many forms of *Dahlia*, *Aster*, *Helianthus*, *Doronicum*, *Inula*, etc., are cultivated for their showy flowers.

Salicaceæ

Characters. *Diœcious shrubs or trees* frequently producing suckers and having *simple*, stipulate and *alternate* leaves.

Inflorescence a unisexual catkin. Flowers (Fig. 140) *hypogynous and borne in the axils of bracts*; perianth rudimentary (poplar) or absent (willow). ♂ flowers (Fig. 140) with two to three (willow) or more (poplar) stamens. ♀ flowers

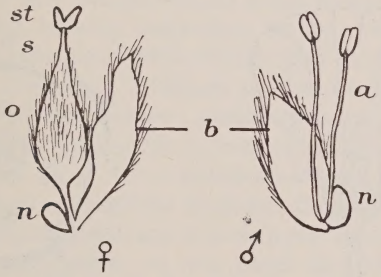

Fig. 140.—Pistillate and Staminate Flowers of Willow (*Salix caprea*). *b*, bract; *a*, stamens; *n*, nectary; *o*, ovary; *s*, style; *st*, stigma.

(Fig. 140) *bicarpellary* and *syncarpous*; stigma bilobed; *ovary unilocular with two parietal placentas bearing many ovules. Fruit a capsule* with non-endospermic *hairy seeds.*

Floral Formula. P 0 or reduced A 2 – ∞ G (2).

Pollination. *Salix* (willow) has a small nectary (Fig. 140) in each flower and is pollinated by insects. *Populus* (poplar and aspen) has a cup-shaped structure which is variously regarded as a rudimentary perianth or a modified nectary, but no honey is produced and pollination is by means of wind.

British Plants. The genus *Salix* includes the different kinds of willows, osiers and sallows. *S. herbacea* is a small alpine willow in which little wood is developed. *Populus* includes the aspen and the various kinds of poplars.

Allied Families. The families Cupuliferæ (oak, chestnut, beech) and Betulaceæ (birch, hazel, alder, hornbeam) also bear catkins (Fig. 84), and are sometimes grouped with Salicaceæ in the order Amentiferæ. Figs. 4, 68, 73 and 84 refer in part to some of these plants.

MONOCOTYLEDONS

Liliaceæ

Characters. Mostly herbs perennating (Figs. 24, 25) by means of bulbs (garlic, onion, hyacinth, tulip), corms (meadow-saffron), or rhizomes (Solomon's-seal). The only British

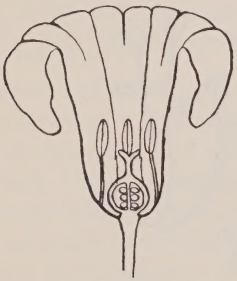

Fig. 141.—M.V.S. of Bluebell Flower.

Fig. 142.—Fl. D. of Liliaceæ.

species which is shrubby is the butcher's-broom, but *Dracæna* and *Yucca* are often cultivated and have a kind of secondary growth. Leaves usually radical, sheathing, lanceolate and isobilateral. Inflorescence usually a raceme, but sometimes cymose as in the onion with cymose umbels. *Flowers* (Figs. 141–2) *regular, perfect, hypogynous, trimerous. Perianth of six parts*, polyphyllous (perianth segments separate) or gamophyllous, *petaloid* (like petals). *Stamens six*, sometimes epiphyllous (fixed on the perianth segments), anthers usually introrse. *Pistil tricarpellary, syncarpous*; ovary trilocular with *many anatropous ovules on an axile placenta* (Fig. 116). Fruit usually a capsule. Herb Paris, Solomon's-seal, lily-of-the-valley and asparagus have berries. Seeds endospermic.

Floral Formula. Typical:

$$P\overset{\frown}{3} + 3\ A\overset{\frown}{3} + 3\ G\underline{(3)}, \text{ or } K\ (3)\ C\ 3\ A\ 3 + 3\ G\ (3).$$

Herb Paris: $P\ 4 + 4\ A\ 4 + 4\ G\underline{(4)}$ is the usual one.

Pollination. Entomophilous (insect-pollinated). The flowers are usually showy and honey is sometimes formed. In the bluebell the nectaries are in the partitions between the three chambers of the ovary, in the lily at the bases of the perianth segments. The flower of Herb Paris has a fœtid smell and is pollinated by flies.

British Plants. Bluebell (Fig. 141), star-of-Bethlehem; Solomon's-seal with broader leaves borne on the stem; lily-of-the-valley with broadly lanceolate leaves; May lily (*Maianthemum*), a rare plant with cordate and cauline leaves and flowers often dimerous; fritillary and wild tulip with flowers usually terminal and solitary; garlic, ramsons, leeks, in which bulbils sometimes replace the flowers (Fig. 32); bog asphodel with long seeds (Fig. 72); butcher's-broom with unisexual flowers and ovate-lanceolate cladodes (Fig. 30); asparagus, with needle-like cladodes and minute scaly leaves; Herb Paris with four broad leaves on the stem and flowers usually tetramerous; and meadow saffron, which flowers in the autumn, fruits in the spring, and has a very long perianth tube enclosing three long styles.

Cultivated Plants. Lilies, tulips, hyacinths, etc., are grown for their showy blooms; *Dracæna*, *Aloe*, *Aspidistra* and *Yucca* for their foliage, and onions for their bulbs; *Smilax* is the sarsaparilla plant and has stipule tendrils. In *Lilium bulbiferum* vegetative reproduction occurs by bulbils (see Fig. 31).

Allied Families. Liliaceæ is placed with Juncaceæ, Amaryllidaceæ and Iridaceæ in the order Liliales. The first is the rush family and differs from Liliaceæ in having a sepaloid perianth. Amaryllidaceæ has an epigynous flower and emergences from the perianth often unite to form a cup or bell (corona) which is very prominent in the daffodil. In

Iridaceæ, to which the *Iris* and *Crocus* belong, the flower is epigynous and the three inner stamens are suppressed.

Orchidaceæ

Characters. Perennial herbs with rhizomes (helleborine), or tubers (*Orchis*, *Ophrys*). Leaves usually lanceolate, sheathing and parallel-veined as in other monocotyledons. In some the leaves are ovate (broad-leaved helleborine) or cordate (tway-blade), whilst in the saprophytic bird's-nest orchid,[1] coral-root, and a few other rare species they are reduced to brown sheathing scales. Inflorescence racemose, usually a spike. *Flowers* (Figs. 88 and 143) *irregular, perfect, epigynous.* Perianth petaloid, the posterior *petal* (*labellum*) *becoming enlarged and anterior* in mature flowers, owing to the *ovary twisting through* 180°. The essential organs are borne on a *central column* (gynostemium) and the flower is said to be gynandrous. Stamens reduced to one or two; in most species there is *one stamen*, whilst there are *two toothed or lobed prominences* (*staminodes*) representing the anterior stamens of the inner whorl; in the lady's slipper (*Cypripedium*) a reverse condition occurs, the staminode is outer and anterior, whilst the two anterior and inner are true stamens. Each stamen has two *prominent anther-lobes, each occupied by a pollinium* (Fig. 88), with a stalk (caudicle) and a basal disc (glandula). In *Cypripedium* the pollen-grains are sticky, but are not aggregated into pollinia. *Pistil tricarpellary, syncarpous*; ovary unilocular, with *many anatropous ovules* (not developed till after pollination) on *three parietal placentas*; stigmas three, the central one usually transformed into a short beak (rostellum), the two lateral more or less confluent and forming *one stigmatic surface.* In *Cypripedium* the three stigmas are fused and there is no

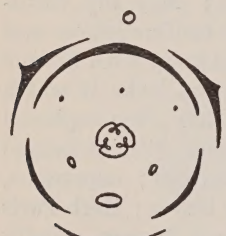

Fig. 143.—Theoretical Fl. D. of Orchidaceæ. In the actual flower the large petal is anterior.

[1] Often with mycorhizæ (see p. 171).

rostellum. *Fruit a capsule* with a large number of *minute seeds.* Seed non-endospermic; embryo not differentiated into plumule, radicle and cotyledon.

Floral Formulæ. *Orchis*: $\downarrow$ P 3 + 3 $\overbrace{\text{A}\,1 + 0\,\text{G}}$ $\overline{(3)}$.

Cypripedium: $\downarrow$ P 3 + 3 $\overbrace{\text{A}\,0 + 2\,\text{G}}$ $\overline{(3)}$.

Pollination usually entomophilous. Usually no honey is excreted (free honey in spur of *Habenaria*), and the insect has to pierce the tissue at the base of the labellum to obtain it. The enlarged labellum (Fig. 88) forms a landing-stage for the insect. The general method of pollination has been described on p. 123. In some plants, e.g. bee orchid, self-pollination is the rule. The butterfly orchid is fragrant in the evening and is pollinated by moths. Wasps pollinate the helleborine.

British Plants. Most of our common wild orchids (spotted, early-purple, pyramidal, marsh, green-winged) belong to the genus *Orchis* (Fig. 88) and have the lip or labellum spurred. *Habenaria* also has the lip spurred, but its species (butterfly, fragrant, and frog orchids) are rarer and the glandulæ are not enclosed in a pouch as they are in *Orchis*. The bird's-nest orchid is saprophytic (see p. 171) on decaying leaves of beech, hazel, etc., and has brown scales and flowers. Tway-blade has greenish flowers and two large leaves. Bee orchid and lady's-tresses are not uncommon in limestone districts.

Foreign Plants. Many species are cultivated in greenhouses. Many tropical and sub-tropical members of the family are epiphytic, clinging by adventitious roots and sometimes provided with aerial roots with spongy tissue at their apices for absorption of atmospheric moisture. *Vanilla* provides a well-known flavouring.

Gramineæ

Characters. Annual or perennial herbs with *hollow internodes, swollen nodes* and *intercalary growing points* above the nodes. *Leaves alternate, distichous* (Fig. 45), with long,

sheathing bases, which are *split on the side opposite the leaf-blade*, and linear or lanceolate leaf-blades, each *with an outgrowth* (*ligule*) *at its base* (Fig. 45). Inflorescence often complex. The unit of inflorescence is a *spikelet* (Fig. 145), which is a small group of one or many flowers sessile on a slender axis (rachis or rachilla). At the base are two bracts without flowers and these are the empty glumes. Above these are one or more bracts (flowering glumes), each with a flower in its axil. A second bract is usually present on the inner side of the flower, so that the latter is enclosed within two glumes, the outer or true flowering glume and the inner flowering glume or pale. The flowering glume often has a long process (awn or arista) and the pale is often much smaller than the other bracts. The

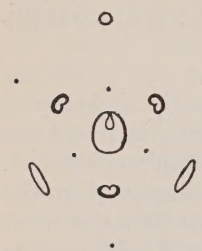

FIG. 144.—Theoretical Fl. D. of Gramineæ.

The ellipses in the antero-lateral positions represent the scales (lodicules).

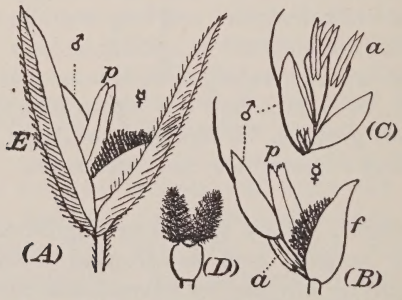

FIG. 145.—Inflorescence and Flower of a Grass.

—*Holcus lanatus* (× 6). *A*, spikelet. Two empty glumes *E* enclosing two flowers, a perfect and a staminate. *p*, pale; *f*, flowering glume. *B*, empty glumes removed. so as to expose the lower perfect flower and the upper staminate one. The flowering glume of the staminate flower is awned. Filaments of stamens (*a*) of perfect flower have not yet lengthened. *C*, ♂ flower with three stamens (filaments not fully lengthened). *D*, pistil.

spikelets are arranged in spikes, racemes or panicles. The panicles may be close and cylindrical as in the foxtail or effuse and loose as in the common meadow grass. *Flowers*

(Figs. 144–5) usually perfect, *hypogynous*, and with perianth absent or much reduced to scales (lodicules). *Stamens usually three*, but sometimes further reduction to two occurs (e.g. sweet-scented vernal grass), *filaments long*, anthers large, loosely-hinged (*versatile*) and splitting towards the outside of the flower (extrorse). Pistil nearly always reduced to one *carpel with two feathery stigmas*. *Fruit a caryopsis* containing endosperm.

Floral Formula. P 0 or reduced A 3 + 0 G (1–2).

Pollination. Anemophilous (wind-pollinated). The flowers are mostly protogynous, the stamens have long filaments and large versatile anthers and the stigmas are long and feathery.

British Plants. The following are the most common or show some interesting peculiarity: Bent grass (*Agrostis*), cock's-foot grass, meadow grasses (*Poa*), fescue (*Festuca*), melic grass (*Melica*), reed (*Phragmites*), couch grass (*Agopyron*), a pestilent weed owing to its slender rhizomes, quaking grass (*Briza*) with ovate spikelets, tussock grass (*Deschampia*), barley (*Hordeum*) with very long awns, blue-moor grass (*Molinia*), a grass of wet heaths, marram grass (*Ammophila*) of sand-dunes, brome grasses (*Bromus*), floating meadow grasses (*Glyceria*), cord grass (*Spartina*) on salt marsh. Yorkshire fog (*Holcus*, Fig. 145) has two flowers in the spikelet, but the upper one is staminate only. False oats (*Arrhenatherum*) is similar in this respect, but the staminate flower is the lower one. Mat grass (*Nardus*), a moorland plant, has no empty glume and there is only one stigma. Rye grass (*Lolium*) has only one empty glume, the purpose of the other being served by a hollowed-out rachis. Dog's-tail grass (*Cynosurus*) has some of its flowers sterile and the bracts are deeply toothed. Foxtail grass and timothy grass have close cylindrical panicles.

Cultivated Plants. Wheat, oats, barley, rye, etc. Maize or Indian corn has solid internodes. Rice, millet and the sugar-cane are cultivated in tropical or sub-tropical regions. Bamboos are woody and form trees.

Allied Family. The sedge family (*Cyperaceæ*) is included with Gramineæ in the order Glumifloræ. The sedges (Fig. 22) are similar to grasses in many respects, but the leaf-sheaths are not split, the stems are usually solid and triangular, the spikelet is less complicated, and the pericarp is not coherent with the testa.

CHAPTER XXII

ECOLOGY—THE PLANT AND ITS ENVIRONMENT

A celebrated naturalist is said to have tried to grow an unknown plant which had been sent to him. He tried it in various parts of his garden, but none of the situations seemed to suit it. He then put it in a greenhouse, but soon found that the hot conditions were harmful. As a last resort he placed it in an ice-house and it soon began to grow vigorously. The story illustrates a fact which is known to every observant field botanist, gardener or farmer. Some plants like particular kinds of environments and will grow better under such conditions than under any others. A gardener prepares his onion bed in a different way from the ground where carrots will be sown, a farmer knows that the conditions suitable for his ripening wheat are not favourable to a developing root-crop, and a field botanist does not expect to find a bee-orchid and a foxglove growing together.

Systematic Ecology. The housing of plants was studied and much information about it was obtained before the twentieth century, but its systematic study is a development of recent years. The study of all the factors which affect the housing of a plant is known as plant-ecology. A good ecologist must have a wide and accurate knowledge of the names of plants, must know where they grow, how they are associated together, how they are able to grow in their particular habitats and must consider all the factors which have contributed to the establishment of a plant in its particular habitat.

Necessity for Field-Work. Ecology is not a subject

which can be taught from a book ; some help may be afforded by a chapter on it, though, if it were possible, that chapter should be written to suit the locality of each reader. Field-work is the most essential as well as the most interesting part of the subject. Physiological experiments in the laboratory may supplement the field-work and agreement should be obtained between the results in the laboratory and those in the field. If discrepancies occur the laboratory work should be regarded with suspicion, as in the artificial manipulation of the material incorrect or incomplete answers to the experimental questions may be given.

Habitat. The term habitat is generally and quite correctly used to mean the place of abode. The habitat of a plant is the place where it lives, but an ecological concept of the term has a wider significance. It refers not only to the place of abode but also to the conditions determining the establishment of a plant or of a plant community at that particular place. We may then speak of habitat factors and we may to some extent estimate the importance of these factors in conditioning the life of the plant. The habitat factors may be placed in four different groups :—climatic, physiographic, edaphic and biotic.

Climatic Factors. These are concerned in producing the climate of the region and therefore refer to temperature, humidity and movements of the air, rainfall, light, etc.

Physiographic Factors. These are determined by geological or topographical features, such as arrangement of the strata, drainage, slope, altitude, deposition of sediment, movements of sand and erosion.

Edaphic Factors. These refer to the physical and chemical constitution of the soil and include such things as the size of the soil particles, the presence or absence of calcium carbonate, the amount of water present, and the facility with which aeration is effected.

Biotic Factors. These are due to the action of animals or plants.

Combined Action of Factors. All these factors are

concerned in the preference [1] of a plant for a particular spot. If a particular species is studied in the field its healthy life may be shown to be dependent on some of the factors of all these different groups. For example, let us take the foxglove. The climatic factors of temperature and light influence it to a great extent. It will not grow well when the conditions are extreme in regard to these two factors, a moderate temperature and a slight amount of shade seem to suit it best. A physiographic factor such as the deposition of mud or sand adversely affects the foxglove, whilst moderate altitude and a certain amount of slope appear to be favourable. Amongst edaphic factors the presence of limestone is almost inhibitive of the foxglove, and its poisonous nature, which prevents it from being injured by browsing animals, may be cited as a biotic factor. These various groups of factors are not independent of each other, e.g. the climatic factor of rainfall and the physiographic factor of slope have a great influence on the edaphic factor of water-content, and again a biotic factor may modify it by altering the consistency of the soil.

Influences of Factors on the Life of the Plant

In estimating the influences of these habitat factors we must always consider their effects on the life of the plant. In general they can be resolved into the effects which they exert on osmosis, photosynthesis, respiration, transpiration, metabolism, growth and reproduction. The main factors to consider are temperature, light, wind, water-content and physical and chemical properties of the soil.

Light. Light is necessary for the photosynthetic activity of plants, for the maintenance of the " tone " or healthy state in a plant, and for the direction of many plant-movements. Plants deprived of light become sickly-looking, their stems

[1] This is a teleological way of putting it. As a matter of fact the plant exercises no preference, the environment determines whether it flourishes or not. Such teleological modes of expression are, however, often allowed for the higher animals when there is no evidence that the animal has consciously or voluntarily chosen a certain course.

are drawn out and their leaves remain small, and such plants are then said to be **etiolated**. The loss of tone and the small leaves in etiolated plants are probably due to the interference with the general feeding of the plant, whilst the lengthening of the stem is probably due to the same cause which effects the heliotropic curvatures of plants. In heliotropism light retards the increase in size of the cells of the stem nearest to the light, that side becomes shorter and a curvature follows. In etiolated plants the retarding action of light is absent and the stem is drawn out. Plants which grow in the shade frequently have larger and thinner leaves with poorly developed palisade tissue, and longer stems than sun-plants, but it does not follow that all these characters are directly due to the lesser intensity of light, the greater and more even water-content of the shaded soil, the more constant temperature, and the humus derived from the decay of the leaves falling from the canopy above are contributory causes.

Another modification frequently shown is the apparent distichous arrangement of the leaves. In the same plant (e.g. whortleberry) growing both in the open and in the shade we may see the radial arrangement distinctly shown in the open, whilst the leaves appear to be distichous in the shade. When the canopy of a wood becomes so dense that little light passes through, as in a beech wood, vegetation is almost limited to plants without chlorophyll. The amount of shade can be approximately estimated by means of a photographer's actinometer. The time taken by the sensitive paper to match the standard tint is found for the shade and then for the open. The results may be expressed as a fraction $\frac{\text{Time in shade}}{\text{Time in open}}$; or as a percentage, taking the time in the open as 100. Some plants which are usually hedge plants may grow quite as well in an open situation if a sufficient supply of water is ensured. For example, the woody nightshade usually grows in a shady place but will grow quite well by the margin of a pool.

Temperature. The effects of heat are evidenced by the number of tropical plants which cannot be grown in this

country unless they are put in a hothouse. Some semi-tropical plants are able to grow in the milder portions of the south-west of England and Ireland, and on the other hand a few of the subarctic plants occur in the North of Scotland or on the heights of the Grampians.

Plants are sometimes said to have a minimum temperature below which growth ceases, an optimum temperature at which growth is best, and a maximum temperature beyond which no growth occurs. This is only true in a limited sense since other factors as humidity, light, food and air supply must be taken into account. Variations in these factors may cause the optimum temperature to vary. Similarly in regard to other factors there is no definite optimum for a particular factor; an optimum supply of carbon dioxide to a plant has a greater value at one temperature than at another and the optimum value of water-supply will vary according to other conditions.

Wind. The effect of wind is often well shown on ridges, the vegetation of the more sheltered side being often much richer than that of the side exposed to the prevalent winds. The one-sided appearance of bushes and trees is commonly attributed to the driving action of the wind but is mainly due to the increased transpiration on the windward side. The buds on the exposed side cannot develop whilst the buds on the sheltered side can; consequently the shrub assumes a one-sided appearance.

Soil. The physical and chemical constitution of the soil is well-known to have a great influence on the nature and quantity of vegetation. The rich vegetation of an alluvial plain offers a remarkable contrast to the paucity of the flora on the thin soil resulting from the weathering of hard rocks.[1] The relative importance of physical and chemical characters is a difficult subject, some ecologists believing that physical characters rather than chemical ones are the main determinants in the distribution of plants whilst others hold that,

[1] Two local districts may be contrasted. For Devonshire the valley of the Exe and the granitic soil of Dartmoor are suitable.

in certain cases, the reverse is true. The question is complicated owing to the difficulty of isolating and comparing the two factors, since other factors have to be considered as well. At any rate, whether the calcium salts exert a direct influence or whether the influence is an indirect one owing to the physical characters associated, there is a general difference between the vegetation of a district rich in limestone and of one where the calcium content is low or absent. Some plants are apparently lime-inhabiting or calcicolous, some (calcifuge plants) are usually found where the calcium content is low or absent, whilst others are found either in siliceous or calcareous soil.

Calcicole and Calcifuge Plants. The following plants are characteristic of limestone soils: white beam, spindle tree, ash, spurge-laurel, dogwood, privet, old man's beard (*Clematis*), wayfaring tree, yew, bloody crane's bill, bird's-eye primrose, columbine, rock-rose, yellow centaury (*Blackstonia*), purging flax, mountain St. John's-wort (*Hypericum montanum*), vervain, hairy violet, salad-burnet, crosswort, wall-lettuce, squinancy-wort, greater knapweed, ploughman's spikenard, lesser scabious (*Scabiosa columbaria*), clustered bluebell (*Campanula glomerata*), hoary plantain, wood-spurge, marjoram, kidney-vetch, horse-shoe vetch (*Hippocrepis comosa*), madder (*Rubia peregrina*), mountain bedstraw (*Galium asperum*), fœtid iris, pyramidal orchid, fly orchid, bee orchid, lily-of-the-valley, pendulous sedge, *Avena pubescens*, *A. pratensis*, *Koeleria*, erect brome, *Brachypodium pinnatum*, *Sesleria*, scaly fern and mountain polypody.

The following plants are calcifuge: sweet-chestnut, foxglove, mountain-ash, sheep's-sorrel, gorse, broom, needle-whin, crowberry, heather, ling, whortleberry, birch, sessile-fruited oak (*Quercus sessiliflora*), tuberous-rooted bitter-vetch (*Lathyrus montanus*), ivy-leaved bluebell, sheep's-bit (*Jasione*), *Luzula multiflora*, *Juncus squarrosus*, *Carex binervis*, *Deschampia flexuosa*, *Molinia cœrulea*, *Nardus stricta*, bracken, hardfern, and *Lastrea oreopteris*.

In a limestone district patches of vegetation, in which calcifuge plants are present, occur but these apparent excep-

tions are due to the **leaching** or washing out of the soluble salts and little or no calcium salt is present in the upper layers of soil. In some cases the leaching is very superficial and some deep-rooted calcicolous species are intermixed with shallow-rooted calcifuge plants.

Chemical Factors. Many bryophytes and lichens similarly prefer or avoid calcareous rocks or soil and in many cases there seems to be no option to regarding the determining factor as a chemical one. Amongst the most pronounced calcifuge plants are the various species of bog moss (*Sphagnum*).

The injurious effects of lead or copper on vegetation is markedly shown in some districts where mining is carried on. Above the outlet from the mine the outstanding stones and islets in the stream are clothed with mosses and other vegetation, whereas those below the outlet are quite bare. These effects are very evident in the river Rheidol near Aberystwyth, where lead mining causes the pollution, and in the stream which comes down from the copper mines near the Old Man of Coniston.

The Different Layers of Vegetation. In a particular association the plants are not living under the same conditions. This has been shown above in the case where shallow rooted calcifuge plants are growing with deep-rooted calcicole plants on a superficially leached soil. It is also evident that in any association the shorter plants are more shaded, have a less light supply and less evaporation than their taller neighbours. In a wood the ground flora is protected by the canopy of foliage from the overshadowing trees ; in a marsh there may be several layers of vegetation, an uppermost of grasses or sedges, an intermediate of herbaceous plants with dorsiventral leaves, and a lowermost stratum of mosses and liverworts. Then again the plants may not appear at the same time, some plants may have finished their season when others are only beginning. This is often very striking in a cornfield, many of the common weeds of arable land such as fluellen, corn-mint, speedwells and corn woundwort are unable to flourish until the corn is cut.

CHAPTER XXIII

ECOLOGY—ADAPTATIONS TO ENVIRONMENT—PLANT-ASSOCIATIONS

Adaptation to Habitat

There is such a keen competition amongst plants that only those which are most fit to live in the particular habitat are able to survive. A plant which grows in a poor soil does not necessarily prefer a poor soil; it may have been pushed out of the better soils by the competition of other plants. Its conquerors are, however, unable to compete with it for the possession of the poor soil. Most land plants are able to live a healthy life if placed in good garden loam and if the competition of other plants is checked; but if this competition is unrestrained many species of plants are unable to exist. For instance:—the gardener must weed vigorously if he wishes to get a good bed of asparagus. In fact he usually sprinkles salt over the soil as if he were manuring the asparagus. What he actually does is to make the conditions less favourable to the weeds which were growing with the asparagus. The asparagus in its natural habitat is a plant of salty soil, is able to endure a greater concentration of salt in the ground water, and is therefore said to be adapted to its environment. The bindweed is another example of adaptation to environment, as it twines round the stalks of the corn among which it grows.

Wall-Plants. The plants growing on a soil-capped wall show adaptations [1] to their environment. They are con-

[1] Adaptation can be used in two ways: (1) A species may have constant characters which fit it to live in a particular place. (2) An individual may become adapted to its environment by the development of some character which is not usually present in other individuals of the species. This kind of adaptability is often termed modifiability.

fronted with one great difficulty, and that is a constant supply of water. At certain seasons and times there is an abundant supply whilst at others water is almost entirely absent, and it is just at this time of drought that the plants are exposed to greater temperatures and light-intensities than the plants growing at the foot of the wall.

Adaptations to Dryness. The stonecrop and pennywort provide for the time of drought by having thick leaves which take up a large amount of water when occasion offers. In the vernal whitlow-grass or in the thale-cress, the germination of the seed, the growth of the plant, and its flowering and fruiting take place in the early part of the year before

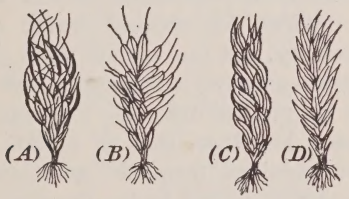

FIG. 146.—Xerophytic Adaptation.

Mosses with leaves twisted during dry weather (× about 10). *A* and B, *Tortula muralis* in dry and wet condition respectively. *C* and *D*, *Grimmia torquata* in dry and wet condition respectively. In *A*, the leaves are curled during dry weather so that the hair-points and midribs only are exposed.

the lack of water is likely to become serious. Some plants adapt themselves to dry conditions by devices for reducing the loss of water. The hairy bitter-cress and the mouse-eared chickweed are thickly clothed with hairs, some grasses roll their leaves (Fig. 112) and some mosses curl and twist their leaves round each other so that only the midribs are exposed (Fig. 146). The dyer's-weed and dandelion are able to exist on walls because of their rosette habit, a larger area being available for the supply of water; the former also has its transpiration retarded by the crinkly character or waviness of its leaves.

Most wall plants have a thick cuticle to the upper epidermis of the leaf, the guard-cells of the stomata are sunk below the

level of the adjacent and projecting epidermal cells (see Fig. 168, *C*) and in some cases a waxy coating is a further preventative against undue evaporation. In some lichens (*Collemas*) common on walls the thallus contains mucilage which can absorb water during a rainy time (see Figs. 224–5).

Plants which grow on walls and in other habitats which cause them to be exposed to long periods of drought are known as **xerophytes.** At the opposite end are the **hydrophytes**, which grow in the water, whilst the plants which grow in medium conditions in regard to water-supply are termed **mesophytes.**

Hydrophytes and Gas-Supply. Hydrophytes, or plants which live in water, apparently have as much water as they require. If there is no hindrance to the intake of water none of the devices for storing water or reducing its output are necessary, but one of the main problems will be the intake of gases as oxygen is required for respiration and carbon dioxide for photosynthesis. The solubility of oxygen in water is much less than that of carbon dioxide, and if these gases are obtained from the solutions in water, the difficulty is greater in regard to the oxygen supply. It does not seem to be absolutely necessary for these gases to be taken from their solutions in water. During the daytime when light conditions are suitable photosynthesis occurs and some of the waste product (oxygen) can be used in the respiratory process. If photosynthetic activity is small, the processes of respiration and photosynthesis may balance each other; the waste carbon dioxide of respiration supplying that required for photosynthesis and the waste oxygen of photosynthesis supplying that required for respiration. This balance is seldom attained; there is usually an excess of oxygen which bubbles through the water, and a deficiency of carbon dioxide, consequently the photosynthetic activity is limited. At night the carbon dioxide is in excess and the oxygen is deficient. The activity of a plant which obtains its gases from solution in the water is then limited by the power the water possesses of dissolving the gases, unless some method for storing the gases occurs. If the excess oxygen

of the day can be stored till night it is available for respiration, and if the excess carbon dioxide of the night can be stored till light conditions are suitable, it is available for photosynthesis. Many water plants contain a large amount of intercellular space (Fig. 147) in which such storage may occur.

Thin and finely divided leaves (Fig. 117) have a greater surface area in regard to bulk than thick and undivided ones, and water plants usually have such leaves. When the leaves are submerged, stomata are unnecessary, but when

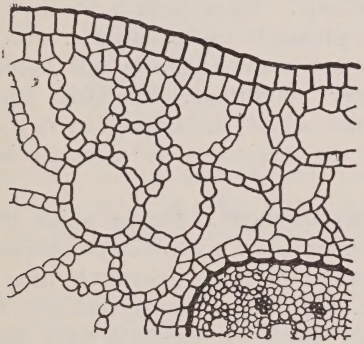

Fig. 147.—Aquatic Stem.

Portion of stem of *Potamogeton crispus* showing air-spaces and reduced vascular and stereom tissue (× about 40).

they are floating stomata are usually present on the upper surfaces. When the plant is supported by the water, less mechanical tissue is required, and as the water-conducting system does not need to be strongly developed, the xylem is often little evident (Fig. 147).

Groups of Hydrophytes. There are at least four groups of hydrophytes: (1) Completely submerged plants (e.g. pondweeds).[1] (2) Floating plants which have no roots fixing them to the soil (e.g. duckweeds, Fig. 16). (3) Rooting plants with floating leaves and usually also with submerged

[1] In some pondweeds the inflorescence rises above the water.

leaves, which are often of a different shape from the floating ones (e.g. some species of water-crowfoot). (4) Plants at the margin of the water. The common reed-grass is an example, and this association of plants is often called a reed-margin one. As a rule the plants of the reed-margin are monocotyledons with erect isobilateral or centric leaves (e.g. flag, bur-reed, reed-mace, bulrush, flowering rush, and many rushes, grasses and sedges).

Mesophytes. These are a very variable group comprising all those which are not hydrophytes or xerophytes. Some plants which are usually hydrophytes may occasionally become land plants. When a pool becomes smaller, many of the aquatic plants it contained, e.g. water-crowfoot and watercress, do not necessarily die but become adapted to life under drier conditions. Similarly some mesophytic plants sometimes adapt themselves to dry conditions and show some of the structures we associate with xerophytic vegetation.

Physiological Dryness. Plants which grow in marshes or bogs sometimes show hydrophytic characters, especially in the development of tissue (**aerenchyma**) with abundant air-spaces (Fig. 148), but curiously enough, they sometimes show characters which we associate with xerophytes. Bog St. John's-wort (*Hypericum elodes*), great willow-herb and water-mint have hairy stems and leaves. Rushes have their transpiring surface reduced and the cuticle is well-developed (Fig. 148). Many sedges have their leaf margins recurved, and their stomata protected or sunk. The leathery and waxy leaves of the cranberry and marsh andromeda have their margins strongly recurved, whilst in the cross-leaved heath (*Erica tetralix*) they become rolled round so much that the under surface is almost concealed (see Fig. 149). Similarly, xerophytic devices are adopted by plants growing in sour or saline soil which is rich in osmotic substances.

One theory which has been formulated to explain the occurrence of plants with xerophytic devices in wet situations is that of physiological dryness. The water is present around the plants but cannot be taken up in sufficient quantities to

meet their needs unless devices for conserving the water or reducing its output are present. Osmosis is interfered with

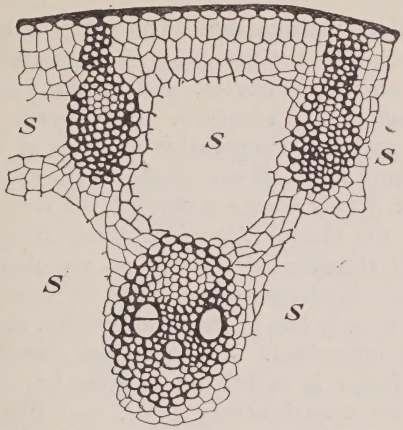

Fig. 148.—T.S. of Soft Rush (*Juncus effusus*).

Lysigenous air-spaces (*s*) produced by the rupture and drying up of cells. Bars of sclerenchyma connect the outer fibro-vascular bundles with the epidermis. Cuticle well developed. (× about 150.) The stem of the soft rush functions as a leaf and has a similar structure to that of a centric leaf.

by the lower temperature of the water or by its high concentration of osmotic substances. Possibly some of the xero-

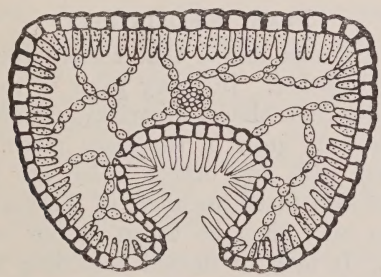

Fig. 149.—Rolled Leaf.

Fine-leaved heath (*Erica cinerea*) with large air cavities. Stomata are in the furrow on the under side and further protection is afforded by the hairs lining the furrow.

phytic devices are ancestral contributions and have no direct bearing on the present habitat of the plant, and in some

cases their chief significance may be to avoid such a concentration in the cell sap as to interfere with the general metabolism.

Ecological Classification. Too much importance must not be attached to the grouping of plants into xerophytes, mesophytes and hydrophytes, and to the interpretation of many characters as adaptive. Field-work, physiological experiments and the comparative analysis of the structural details of plants must all contribute to the study of ecology, and the more deeply they are studied the deeper is the conviction that the classification into three groups is a rough one and that the general theories on structural adaptation are only approximations to the truth. The supply of water to the plant is only one of its requirements, though it is one of the most important. An ecological classification based on a single factor is useful but it must be recognized that it rests on an unsatisfactory basis, and like the Linnean system of plant classification must be regarded as an artificial one. The Linnean system [1] had to give way to a more natural system in which all the characters were taken into account, and the unsatisfactory ecological system mentioned above must be replaced by a more natural one in which all the requirements of the plant are considered.

Plant Associations

Every field botanist knows that certain species of plants are associated together. In many parts of the country the presence of water-cress almost invariably denotes that brooklime and marshwort grow in the same place. These three plants, together with any others which are usually found with them, are said to be members of the same association. An association may then be taken as our ecological unit of vegetation. It may be named according to the habitat or according to the plants most frequently present. It is impossible in this book to deal with the different associations in detail. Some references have already been made to the

[1] The Linnean system of plant classification mainly relied on the number of stamens and carpels.

associations of plants found in water, marshes, bogs, heaths, woods, cornfields, etc., and a more detailed analysis of the associations found near the sea is given below. This will show some of the methods of ecological classification, and for any further details the reader may consult works dealing specially with plant ecology.

Sea-shore Vegetation. The vegetation of the sea-shore shows many associations, and some of these are mentioned below. The physiographical factor of mobility of the material, owing to movements of the water or wind, is an important one in these associations. Amongst edaptic factors the influence of the salinity of the water in causing physiological drought is evidenced by the thick leaves (e.g. sea-aster, samphire, *Sucæda*), waxy covering (e.g. yellow-horned poppy), prickly leaves[1] (e.g. saltwort, sea-holly), reduction of transpiring surface (e.g. sea-rush), rolled leaves (e.g. lyme-grass, marram-grass), restriction of growth to wet season and other xerophytic devices occurring in maritime plants.

Open and Closed Associations. On a muddy shore the pioneer of vegetation is the glasswort (*Salicornia*) which occurs as scattered plants, or scattered patches of plants, and an association of this nature is called an open one. Further inland, the grass *Glyceria maritima*, often intermixed with *Triglochin maritimum*, sea-aster, sea-lavender, thrift, sea-plantain, sea-milkwort and sea-spurge, forms a carpet of vegetation and the association is then a closed one. On the margins of water channels and pools (salt pans), obione (*Atriplex portulacoides*) and *Sucæda* are often abundant. On the Hampshire coast the grass *Spartina* enters largely into the salt marsh vegetation.

Dune Vegetation. When the littoral deposit is sand it is blown inland by the waves, and sand-hills or dunes are formed. These become colonized by vegetation and rendered

[1] The prickly character indirectly enables the plant to live under dry conditions as it prevents browsing animals from eating the juicy parts of the young plant.

stable or fixed. When there is a constant and abundant supply of sand available, fresh mobile dunes are formed on the seaward side, these in time become fixed so that there is a tendency for the dunes to advance on the seaward side, though this is often checked or countered by the erosive action of the waves during high tides or storms, or by earth-movements.

Mobile Dune. The first line of low dunes on the seaward side is often dominated by the sea couch-grass. In this association, in addition to the dominant couch, sand-sedge, sea-purslane and sea-spurge may be abundant. On the higher dunes further inland the dominant plant is the marram-grass, which has a remarkable power of binding the sand and growing up through the sand which is blown over it. The marvellous way in which the roots and stems of the marram-grass bind the sand is well shown in "wash-outs" by the waves and "blow-outs" by the wind. The marram-grass association may consist almost entirely of marram-grass, but other plants, such as sea-couch, lyme-grass, sand-timothy, red-fescue, sand-sedge, sea-spurge, sea-holly, sea-purslane, ragwort and sea-bindweed are often present. The three main fixers of the sand are the marram-grass, sea-couch, and sand-sedge. The underground slender rhizomes (for sand-sedge see Fig. 22) of these plants can be followed out for many yards and are evidenced on the surface by the tufts occurring in lines.

Stable Dune. The blowing of the sand is more or less arrested by the plants in the marram-grass association, and further inland the dunes become more stable and many other species of plants appear. Some of the more widespread species of fixed dunes are sea mouse-ear chickweed (*Cerastium semidecandrum* and *C. tetrandrum*), stork's-bill, creeping rest-harrow (usually the spiny variety), bird's-foot trefoil, hare's-foot trefoil, red-fruited dandelion (*Taraxacum erythrospermum*), mouse-ear hawkweed, creeping thistle, red centaury, and hairy hawkbit (*Leontodon nudicaule*). Some calcicole plants as the kidney vetch, sage, carline-thistle, are able to exist owing to the presence of comminuted shells. Some mosses,

especially *Tortula ruraliformis* and *Camptothecium lutescens*, and some foliose lichens (especially species of *Peltigera*) are important, not only in temporarily fixing the surface of the sand, but also in providing humus to enable the higher plants to grow more vigorously.

Shingle. On some parts of the coast the littoral deposit consists of coarse material and shingle beds are formed. The best examples of such beds are shown at Weymouth (Chesil Beach), Blakeney Point, Pevensey, Dover and Borth. When the pebbles are free from sediment, they are almost bare of vegetation, except a few lichens and mosses, but when mud or sand is mixed an association of shingle plants is formed. The most frequent plants are sea-campion, yellow-horned poppy, beet, wavy-dock (often the var. *trigranulatus*) and various oraches (*Atriplex patula*, *A. babingtonii*, *A. hastata*). Many of these plants have much longer roots than when they occur in other habitats.

CHAPTER XXIV

HEREDITY—VARIATION—EVOLUTION

There is a phrase that "like breeds like" and it is so generally true that we rely upon it in our gardening and farming. One does not expect to gather grapes if thistle seeds are sown, no matter how we grow them. Environment may have some effect on the quantity and quality of the thistle crop, but the crop will still consist of thistles, whatever the environment under which it has been grown. The characters [1] must then have been present in the thistle seed, and as the seed is developed from the egg, they must have been in the egg. As the egg was formed by the union of two gametes, all the characters of the mature plant, unless some have been acquired owing to the influence of the environment, must then have been present in one or other of the gametes. This passing on of the characters from one generation to another is said to be due to heredity.

Variation. Although it is true that the offspring repeats the characters of the parents in a general way, we know that there are differences between them. If we compare the progeny of a pair of cats, we find that one kitten differs from another in minor details, usually sufficiently for the kittens to be recognized from each other. Similarly, if we arrange that the stigmas of the flowers in one plant are pollinated from the stamens of another plant of the same species, the seeds which are formed will produce plants like each other in general characters but unlike each other in some

[1] To be precise one should say the factors which cause the characters to appear. The characters themselves are not manifested till the plant grows.

respects. Some of these variations may be due to the influence of the environment, others may be due to a cause which we shall consider later,[1] but there still remain some which are difficult to explain, unless we assume that there is a tendency to vary.

Evolution. This power of variation was used by Charles Darwin as a foundation stone for his theory of evolution. Before Darwin published his theory of evolution, other naturalists had been struck with the resemblances in groups of organisms and had conceived the idea that members of such a group had evolved from the same ancestor, but it was not until Darwin had published the *Origin of Species* in 1859 [2] that the theory captured the imagination of the scientific world. For twenty years previously, Darwin had been assiduously collecting data and considering probable objections to this theory, so that when it was launched it was supported by a mass of overwhelming evidence. Darwin's particular theory of evolution was natural selection.

We know that there is a lot of competition amongst plants. If a piece of ground is cleared, thousands of seedlings spring up in a space which is often insufficient to support ten. Only those seedlings which have got the best start and are most capable of living under the particular conditions occurring at the place and time will be able to do so, whilst the rest will be eliminated. As every species has a tendency to vary, a comparative examination of one particular character in a number of individuals of the same species, generally shows that some individuals possess that character in a more pronounced manner than the majority, whilst others have that character weakened. Now, if the conditions of life are more favourable to organisms possessing that particular character in excess, those doing so will have the best chance of surviving, and in the course of time will more or less displace their less fortunate neighbours.[3] If the favourable character is con-

[1] Variation according to Mendelian rules.

[2] A joint paper by Darwin and Wallace was given in 1858 but did not attract much attention.

[3] It is taken for granted that the character is inheritable.

cerned with a particular habitat or season, the elimination will only affect those competitors in that particular habitat or during that particular season; all the kinds will live on but some will be forced to grow in other habitats or at other seasons.

Natural Selection. Some of the different species of buttercup (see p. 178) may be used as illustrations of this evolutionary theory. There are three common buttercups (Fig. 54) of our pastures, the acrid, the bulbous and the creeping, and there are also some buttercups which grow in water (Fig. 117). If we suppose that originally there was only one species of buttercup, we know from present-day experience that the individual buttercups were not exactly alike. The stems of some were longer or more erect than the stems of others. Some stems were more thickened at the base than others. The leaves of some were longer and more narrowly cut than those of others. If the possession of a thickened base to the stem proved advantageous, plants possessing that character survived and were able to reproduce. Assuming that the thickened base to the stem was hereditary, the process of natural selection again worked on the progeny, and so the survivors were those with the thickest bases. By the continued repetition of this process, in the course of time, a new species of buttercup with a "bulbous" base to the stem evolved. The possession of the "bulbous" base seems to be a distinct advantage, as it stores reserve-food, and enables the bulbous buttercup to attain maturity before the other competing species.

The evolution of the bulbous buttercup does not necessarily mean that the ancestral buttercup was eliminated; it is still possible for it to exist but it will arrive at maturity at a later time in the season. Possibly the acrid buttercup is near to the ancestral form of our pasture buttercups, but our data are too meagre to allow us to theorize on this question. It is probable that other individuals had longer stems and have given rise to the acrid buttercup, which is mature when the surrounding vegetation is longer, whilst the creeping buttercup has evolved from individuals varying towards a creeping

stem. Some individuals of the ancestral buttercup may have possessed more finely-divided leaves and thus have been able to exist in wet places. A plant which is submerged must absorb the food and oxygen required from the water, and a finely-divided leaf has a greater surface area for absorptive purposes than a broad-lobed leaf of equal bulk. The continuous variation of the buttercup, growing in wet places, towards finely divided leaves will therefore enable aquatic buttercups or species of water crowfoot (Fig. 117) to be evolved.

The wood anemone and marsh-marigold are obviously nearly akin to the buttercup, and we can postulate a common ancestor for these and all other members of the buttercup family. There is no reason why we should limit the theory to the buttercup family, and we may extend it to all forms of life till we reach a common ancestor in a blob of protoplasm.

Darwin's Evidence. Darwin supported his theory by a mass of evidence derived from the geographical and geological distribution of organisms, artificial selection, gradations between organisms, embryology, etc. Much of this evidence was connected with animal life, and the reader is referred to Darwin's own account in his *Origin of Species*, for further details. Whatever may be the fate of Darwin's particular theory of natural selection, we must not forget that his work gave a sound scientific foundation to the theory of evolution, linked up a large amount of disconnected data and thereby enabled great progress to be made in the study of biology.

Continuous Variation. Darwin relied chiefly on small variations continuous in the same direction, but did not attach a great deal of importance to the larger or discontinuous variations known as "sports." A hairy species may produce a hairless individual, a white-flowered species may have an individual with a red flower, or some individuals have double flowers. All such deviations from the type are known as "sports" or mutants.

Mutation. In the early part of this century, de Vries published his theory of evolution of new species by mutation. He considered, and many other biologists agree with him, that

the starting point of a new species was an individual in which a marked deviation from the type suddenly appeared. Of late years, many mutations have been shown to be quite small ones, and it has become more and more difficult to draw a hard and fast line between discontinuous and continuous variation.

Lamarck's Theory. During the early part of the nineteenth century, a theory of evolution which depended on the inheritance of acquired characters was held by Lamarck and a few other naturalists. We all know how the environment of an organism often modifies some of its characters. The blacksmith who wields a heavy sledge-hammer often develops a large biceps muscle, and a plant, which grows in drier places than usual, often develops devices protective against lack of water. Its leaves may be thicker and able to hold more water, or they may be hairier and better able to prevent the escape of water than those of normal plants. Such acquired characters were held by Lamarck and his followers as capable of being passed on, so that new species of organisms were formed. The giraffe was held to have arisen from a browsing animal with a short neck. By continual straining to reach the higher leaves a slight increase in the length of the neck resulted; this was inherited by its descendants who also increased the length of the neck by straining, and this accumulated increase finally resulted in the long-necked giraffe. This crude idea of the inheritance of acquired characters was disposed of when Weismann enunciated the theory of the continuity of the germ plasm. According to this theory some of the cells resulting from the division of the egg (zygote) are immediately isolated and kept distinct from the other cells (somatic) which form the general body of the organism. The isolated cells eventually give rise to the germ-cells or gametes. As the germ-cells are always distinct from the body cells, the environment which causes adaptations in the latter can have little direct effect on the former.

Inheritance of Acquired Characters. Many biologists of to-day have no belief in the inheritance of acquired char-

acters, but some still believe that the germ-plasm is capable of being influenced in an indirect way through the environment, that the germ-plasm is not isolated in the complete way which Weismann enunciated in his theory, and that there is evidence to show that acquired characters can be transmitted to the offspring. Much evidence has been accumulating during the last twenty years to show that some characters, which have been considered as acquired ones, are heritable. A character is supposed to be an acquired one when it appears in an individual as a result of the environment, but even this interpretation of " acquired " is open to question, as it may reasonably be argued that what appears to be an acquired character may be due to a response of the organism to the environmental stimulus, and that the power to respond was inherent but had not previously been stimulated. If this interpretation is held, no characters can be postulated as acquired ones except those which have been acquired through injuries, and no one believes that a man who has chopped off a finger is able to bequeath this loss to his offspring.

Value of Evidence. Almost any experimental evidence in regard to " inheritance of acquired characters " is capable of different interpretations. Supposing that a plant of which the ordinary representatives are and, so far as is known, always have been glabrous, grows in a dry place and that hairs are formed on the plant so that it is protected from undue evaporation. If that plant forms seeds they may be planted in different habitats. If the seed sown in the dry habitat produces a hairy plant, it may be said that an acquired character is inherited, or it may be said that the capacity to produce hairs is present in the plant but is only used when the right stimulus due to a dry habitat is present. On the other hand, if the seed sown in a moister habitat produces the glabrous type, it may be said that the acquired character is not inherited, or that the acquired character is inherited but the environmental stimulus necessary for the transmitted factor to take effect is absent. Thus, evidence of this kind may be used by both sides, and is therefore of little value

in judging the question, though it may be of value in showing the modifiability of plants by environmental stimuli and that plants have greater plasticity than is usually assigned to them. It may seem that tricks or mannerisms are inherited from an ancestor. We often see a person using some trick or mannerism which a parent or grandparent used, but here again the evidence is not reliable, as it is very difficult to say how far such repetitions are due to imitation or mere coincidence or accident. These examples are sufficient to show the difficulties surrounding the question of acquired characters and any further discussion of the subject will be out of place here.

CHAPTER XXV

MENDELISM

During the twenty years following the publication of the *Origin of Species*, the biological world was so much occupied in discussing it that some important experiments described in 1866 and 1867 were completely overshadowed. These experiments were performed by an Austrian monk called Mendel, have been repeated and extended by numerous biologists during this century, and the result of this immense amount of work is included under what has appropriately been termed Mendelism.

Hybrids. Hybrids between two kinds of plants had been studied for many years, and it was generally known that hybrids showed characters of both parents ; for example, the hybrid between the primrose and cowslip usually has the inflorescence and flower-colour of the cowslip, whilst the erect flower-stalk and the size of the flower agree with the primrose. Many examples of hybrids were known and had been studied, but no definite law in regard to the inheritance of characters had been formulated.

Mendel's Experiments. Mendel decided to make experiments with hybrids, and to confine himself to some definite character. His first experiments were with the common edible pea. There are many varieties of this : some are dwarf plants, others are tall plants and require " sticking " to support them ; some plants have green seeds, others yellow seeds ; in some the seeds are smooth-coated, in others they are wrinkled. In one of these experiments, he took a yellow seed, grew it and found that it bred true, that is, the seeds formed by the plant when its flowers were self-pollinated were always yellow. A green seed similarly treated was

also found to breed true, always producing green seeds. He then took pollen from the yellow-seeded plant to the stigma of the green-seeded one (or vice-versa, it doesn't matter which way was followed), allowed the fruit to ripen and the seeds to set. The seeds did not show any evidence of their hybrid origin, being yellow in colour, just as if they had been produced by pollinating the stigma of a yellow-seeded plant with the pollen from another yellow-seeded one. The seeds were sown, and the plants produced were hybrids between the yellow-seeded and green-seeded kinds of pea. Mendel's problem was how the hybrid nature revealed itself. He pollinated the flowers of the plants among themselves, allowed the seeds to ripen and examined them. He found that both yellow and green seeds were formed in the proportion of three yellow to one green. On sowing the green seeds, and pollinating the flowers of the plants produced among themselves, all the seeds formed were green, but on self-pollinating[1] the flowers of the plants produced from the yellow seeds, only one-third of them bred true and produced yellow seeds only. The remaining two-thirds of the yellow seeds produced plants which on "selfing" did not breed true to type but produced yellow and green seeds again, in the proportion of three to one.

Mendel's Theory. He explained these results by stating that there were two factors present in the gametes,[2] one for yellowness and one for greenness, that a gamete can carry only one of these factors, and that the factor for yellowness was **dominant** over that for greenness. If the male gamete carrying the green factor unites with a female gamete possessing the green factor a green seed is produced. If two gametes, each of which is charged with the yellow factor, unite, the seeds are pure yellow; but if two gametes, one of which possesses the green factor, whilst the other carries the yellow factor, unite, the seeds are yellow, but will betray their

[1] Self-pollinating strictly means that the pollen has come from the same flower. For "selfing" in these experiments the pollen need not come from the same flower; it is sufficient if it comes from the same individual.

[2] Mendel gave pollen-grains and egg-cells.

hybrid nature on cultivation and self-pollination. This is illustrated in Fig. 151, where *Y* indicates the plants with yellow-coated seeds and *G* the plants with green-coated seeds. The crossed lines indicate that the yellow-seeded kind was crossed (cross-pollinated) with the green-seeded kind.

Probable Ratios. That these proportions are what might be expected can be shown by using a double pack of patience cards with yellow and green backs and after shuffling and packing them up, placing them out in pairs. There will be fifty-two pairs and approximately twenty-six of these pairs will consist of a yellow and a green back, thirteen pairs will be yellow-backed and thirteen pairs green-backed. It is not necessary in this illustration to have the cards yellow and green backed; the proportions likely to occur can be shown by using the red suits and black suits as an alternative pair of factors. Another method which may be adopted is to shake up two sets of differently-coloured marbles in a bag and pick them out in pairs. The same proportions will approximately be shown, and the greater the number of marbles the nearer will be the approximation to these proportions.

♂ \ ♀	*D*	*R*
D	*DD*	*DR*
R	*DR*	*RR*

Fig. 150.—One Pair of Factors.

Other Mendelian Results. Mendel investigated in a similar way other paired characters of the pea, and found that they behaved in a similar way. On crossing a round and a wrinkled pea, the F_1 generation (see Fig. 151) bore round seeds, whilst in the F_2 generation there were three plants bearing round seeds to one plant bearing wrinkled seeds, roundness being dominant. Similar experiments with tall and dwarf peas showed that tallness was dominant and dwarfness recessive. Thousands of experiments on both plants and animals have been carried out since Mendel's time, and his principles have been found to be of general application, though they have had to be considerably expanded

and modified. His main contribution was in showing that a gamete can only carry one of a pair of factors, whilst the egg may have two factors, one of which is usually manifested in the organism produced whilst the other is latent or recessive. A general method of expressing the probable combinations is shown in Fig. 150, where *D* represents the dominant factor and *R* the recessive, or as it is now put the presence (*D*) and the absence (*R*) of the factor.

Two Sets of Factors. By the same kind of diagram we may also show the probable combinations in the F_2 generation

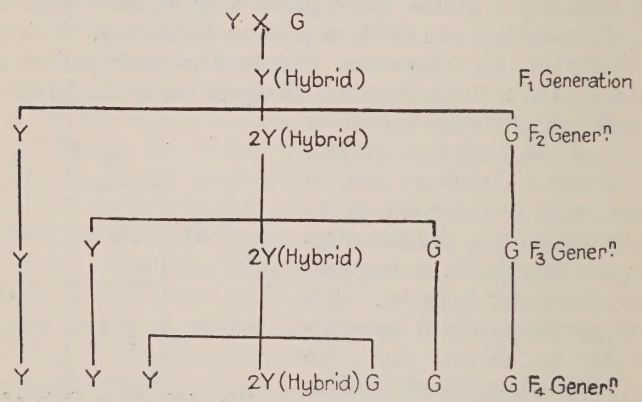

FIG. 151.—Successive Generations when One Pair of Factors is considered.

To illustrate the way in which the plant behaves when "selfing" (see p. 238) occurs, and the names given to the different generations.

when two sets of characters are concerned. If *T* represents the factor for tallness and *t* the absence of this factor whilst *R* represents the factor for round seeds and *r* the absence of this factor, the result is shown in Fig. 152. The four possible associations of the factors in the gamete are *TR*, *Tr*, *tR*, *tr*, and the probable association of the characters in the plants produced are shown in the squares of the chess-board diagram. Nine will be tall plants with round seeds, three will be tall plants with wrinkled seeds, three will be dwarf plants with round seeds, and one will be a dwarf plant with wrinkled

seeds. These proportions of 9 : 3 : 3 : 1 have been shown by experiment to occur in nearly all cases where two pairs (or allelomorphs as they are termed) of characters are considered, and the exceptions have received fairly satisfactory explanations. For experimental verification of the proportions likely to occur when two or three pairs of characters are concerned, several packs of double patience cards can be used.

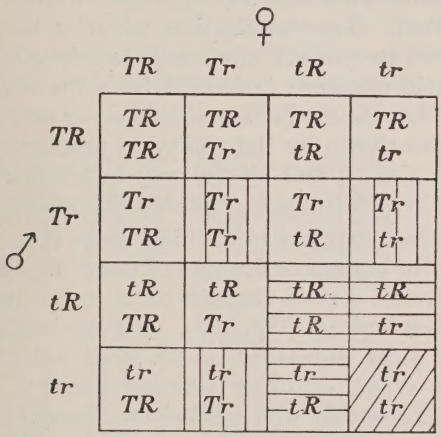

Fig. 152.—Two Pairs of Factors.

For two alternative pairs of factors the different colours of the backs of the cards and the different colours of suits may be used. For three alternative pairs of factors we may use : green and yellow backs, spades and hearts, diamonds and clubs. When three allelomorphs are considered, three or more packs should be used.

Later Results. When three or more pairs of characters are considered, the chess-board method may be used to show how very complicated the question becomes as the number of alternative pairs increases. The question is further complicated by the linkage of factors, so that certain characters are always associated and by the probability that some characters depend on more than one factor. In a fuller consideration

of the progress made in the elucidation of the laws of Mendelian inheritance, references must be made to experiments on Drosophila and other animals, and for further information in regard to these and many other interesting points the reader is referred to the special works dealing with Mendelism.

Situation of Factors. How and where are these so-called factors situated are questions which may be discussed, though it must be remembered that any attempts at answering them are hypothetical. Some mechanism whereby they may be passed on must be present when cells multiply by division, since the whole organism is formed from the division of a single cell. That the mechanism should occur during division of a cell is also shown by the ability to propagate a hybrid by vegetative means, and by the way in which a few cells are capable of vegetatively reproducing the whole organism.[1]

Mitosis. This required mechanism must then be sought in the process of mitosis or division of the cell. When a cell is about to divide, certain changes occur in the nucleus and the adjacent protoplasm (Fig. 153). The nucleus appears to consist of a clear substance which does not stain with hæmatoxylin, eosin, or other staining reagent, and of a substance (**chromatin**) which takes on these stains. In a resting nucleus, these two substances are irregularly mixed, but when division is about to occur, the chromatin assumes a more or less definite thread-like appearance, and ultimately forms a number of small bodies known as **chromosomes.** The number of chromosomes formed depends on the organism but it is definite for any particular species. The nuclei of some species of plants have only four chromosomes, but the nuclei of most of our flowering plants contain three or four times this number. Changes occur in the protoplasm around the nucleus, the membrane of which disappears, and a kind of spindle is formed. This spindle, which is known as the nuclear spindle, consists of cytoplasmic threads or filaments to which the chromosomes are attached at the equator. At this stage the chromosomes are usually somewhat **U** or **V**-shaped

[1] In many of the lower plants even a single cell is capable of vegetatively reproducing the whole organism.

with the open ends directed outwards. The nucleolus meanwhile has disappeared, and the chromosomes have divided longitudinally so that their number is doubled. Then one half of each chromosome moves towards one pole of the spindle, whilst the other half goes to the opposite pole. Two daughter nuclei, each containing the same quantity and also quality of chromosomes of the original nucleus, are then formed at the two poles, the process being the reverse of that which gave rise to the chromosomes, i.e., the identity of the individual chromosomes is lost, the lines of the spindle disappear, the nuclear membrane is formed and nucleolus

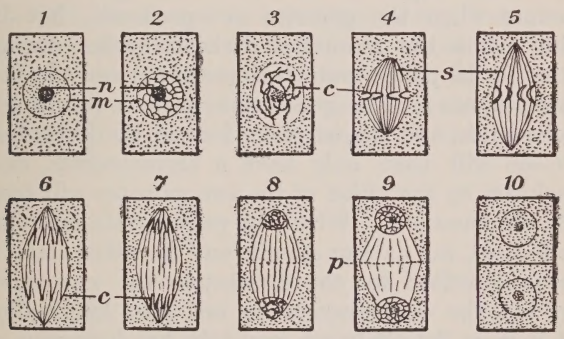

FIG. 153.—Diagrammatic Representation of Mitosis (Karyokinesis).

Successive stages simplified, only four chromosomes shown. *c*, chromosomes; *m*, nuclear membrane; *n*, nucleolus; *p*, cell-plate; *s*, spindle.

appears. The deposition of a cell-wall at the equator of the parent cell usually completes the separation of the two daughter cells. In this process of mitosis, the chromosomes of the daughter nuclei are exactly the same both as regards number and quality, so that if they carry the hereditary factors, equal distribution of the latter is assured, and in this important respect the required apparatus is supplied. We must now see if any modification of the method of division occurs during sexual reproduction, so as to conform with the results of Mendelism.

Doubling and Reduction. During sexual reproduction,

the gametes join together, so that the number of chromosomes in the nucleus of the zygote or egg must be double that in the nucleus of a gamete. If n is the number of chromosomes in the nucleus of the gamete, then the nucleus of the egg will have $2n$ chromosomes. When the egg divides, all the cells resulting will have $2n$ chromosomes, unless some special provision is made in regard to the reproductive cells. If these had $2n$ chromosomes, the next egg would have $4n$ chromosomes, and the number of chromosomes in the plant would be continuously doubled. At some stage in the life-cycle, the number must be reduced so that the gamete contains n chromosomes only. In some of the lower plants this reduction occurs when the gametes are produced, but in the flowering plant the reduction division occurs during the formation of the pollen-grain (**microspore**) and the embryo-sac (**megaspore**). The generative nucleus resulting from the pollen-grain and the oosphere formed by division in the embryo-sac will then only have n chromosomes, and the egg produced by the union of the two gametes will therefore have $2n$ chromosomes. When the pollen-grain and embryo-sac are formed, the nuclear spindle and the other complicated apparatus described for the division in the vegetative cell appear, but the chromosomes do not split longitudinally.[1] To put it more definitely we may take the formation of the pollen-grain in the dicotyledon. The spore-mother cell has $2n$ chromosomes, a reduction division occurs, and 2 nuclei with n chromosomes are formed. A second division of an ordinary kind occurs, and then there are 4 nuclei with n chromosomes; cell walls are then laid down and 4 pollen-grains are formed. The pollen-grain divides as described in Chapter XVIII, so as to form the generative nuclei or male gametes, and, as the divisions are of the ordinary kind, each generative nucleus has n chromosomes.

Meiosis. A similar reduction division occurs during the formation of the embryo-sac, so that the oosphere or female gamete has n chromosomes. On fusion between the generative nucleus and oosphere, the full complement of chromosomes

[1] They may appear to do so. See p. 245.

is restored and the zygote or egg has $2n$ chromosomes. Half of these chromosomes will have come from the male gamete and half from the female gamete, so that the former may be spoken of as the paternal chromosomes and the latter as the maternal chromosomes. As every nucleus in the plant is derived from the continued division of the nucleus of the egg, and as the chromosomes split longitudinally, it follows that any vegetative cell contains n paternal chromosomes and n maternal chromosomes. During the reduction division (meiosis), the paternal and the maternal chromosomes become associated in pairs and a division (which may seem to be a longitudinal one) occurs in each pair, but this is not a splitting of the chromosome into two parts, but simply a separation of the paternal chromosome from the maternal one. Each chromosome, which travels to the poles of the spindle, is therefore a whole chromosome, and not derived from a half-chromosome as in ordinary division.

CHAPTER XXVI

THE FERN AND ITS LIFE-HISTORY

In some parts of the country one of our commonest ferns is the hart's tongue, the young fronds of which are shown in Fig. 42. When it grows in a shady place by the side of a stream its tongue-shaped leaves are frequently over two feet long, but when it grows on a dry wall it becomes dwarfed and its leaves are only an inch or two long. The stunted character of the form growing in a dry habitat indicates that a dry environment is unfavourable and this is generally true for all ferns. The bracken, which is our commonest fern, is a partial exception to this general rule as it often is the dominant plant on some of our dry heaths. The thicker leaves with a well-developed cuticle enable the bracken to outdistance all its other British fern competitors in their invasion of drier ground. On the other hand, the rare filmy ferns (*Hymenophyllum*) have their leaves so thin that they are unable to grow except in wet situations.

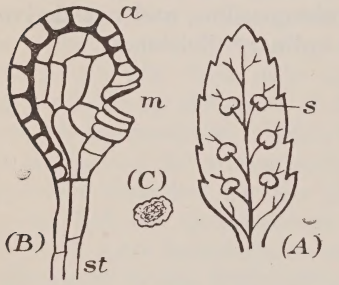

FIG. 154.—Male Fern.

A, Pinna of frond (under surface) with sori (*s*). *B*, sporangium (× 133). *a*, annulus; *m*, stomium; *st*, stalk. *C*, spore (× 133).

Sori. On the under surfaces of the leaves or fronds of all these ferns, bodies (sori) are produced which are brown when mature (Fig. 154, *A*). In the hart's tongue fern, the sori occur as transverse lines between the midrib and the margin ;

in the bracken they occur at the sides of the leaflets and are covered over and protected by the recurved margins, whilst in the filmy fern they are ovoid bodies near the rachis. None of the ferns we have hitherto considered can be taken as our type. The simple leaf and the linear sori of the hart's tongue are not typical of ferns, whilst the bracken and filmy fern form two extremes in regard to their structural adaptations to habitat.

Lastrea as Type. The best fern to take as our type is the male fern (*Lastrea filix-mas*). It is common in many parts of our country and in regard to environment, shape and division of the frond, and the form of the sorus (Fig. 154, *A*) corresponds nearly to what we may regard as an average fern. The following account is therefore chiefly concerned with the male fern, though some references will be made to other ferns which show deviations from the normal structure.

FIG. 155. — Moonwort (*Botrychium lunaria*).

A, barren portion of frond. *B*, fertile portion, showing sori. *R*, adventitious roots (natural size).

Root and Stem. The underground portion of the plant is a rhizome, on which numerous fibrous adventitious roots are developed. From this rhizome radical leaves appear, and as the plant becomes older, the upper portions of some of these leaves decay and their persistent bases form a covering to the lower part of the rhizome. The apex of the rhizome usually reaches just above the surface of the earth, and is covered by young leaves and large brown scales (**ramenta**). Adventitious buds develop on some of the leaf-bases, and may be separated as independent plants owing to the gradual decay of the lower parts of the rhizome. In the bracken, and more especially in the tropical tree-ferns, there is an aerial stem.

Leaf. The leaf is large, bipinnate or almost so, and has

its petiole continued as a rachis almost to its apex, both petiole and rachis being clothed with scales (**paleæ**) similar to the ramenta but smaller and paler. The circinate prefoliation (Fig. 42) and the forked or furcate venation of the leaf (Fig. 154, *A*) are characteristic of ferns. A third feature which distinguishes the leaves of ferns from those of flowering plants is the occurrence of groups (sori) of reproductive bodies on them. In the male fern and most other ferns these sori are borne on the under surfaces of the ordinary leaves, but this is not the case with some ferns. In the hard fern the leaves

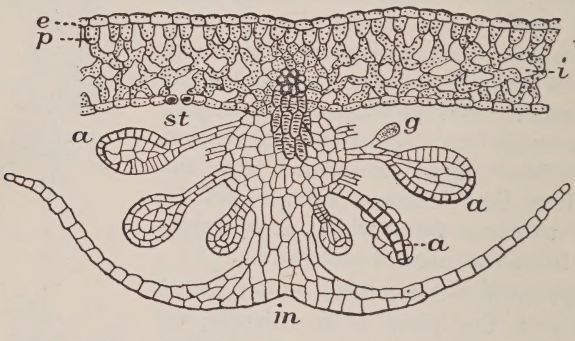

FIG. 156.—Fern.

Section of leaf and sorus (somewhat simplified) (× 50). The sporangia are in different stages of development and are cut through in various ways. The tracheids of the vein are cut through transversely above and obliquely below. *a*, annulus; *e*, epidermis; *g*, gland on sporangial stalk; *i*, intercellular air-space of spongy mesophyll; *p*, palisade tissue; *st*, stoma; *in*, indusium.

bearing the sori are longer and have narrower leaflets than the ordinary vegetative leaves. The flowering fern (*Osmunda*) has the upper leaflets of some of its leaves fertile whilst in the adder's tongue (*Ophioglossum*) and moonwort (*Botrychium*, Fig. 155) the fertile part of the leaf is distinct from the vegetative portion.

Sorus and Sporangium. Each sorus is developed under a vein, and consists of a protuberance on which spore-cases (sporangia) are formed (Fig. 156). As these sporangia contain minute grains (spores) which are capable of germination, the

protuberance is often spoken of as a **placenta**. At the apex of the protuberance, growth continues so that an umbrella is formed over the sporangia. This protective umbrella is known as the **indusium**, is heart-shaped in our type, but is differently shaped or even absent in other ferns. In order that dispersion may be effected some differentiation has occurred in the single-layered sporangial wall. All the cells composing this were originally thin-walled, but thickening occurs along a longitudinal line, so that an incomplete ring (**annulus**) of thick-walled cells is formed. When the spores are ripe and the sporangial wall begins to dry up, splitting is most likely to occur where the ring is left uncompleted (Fig. 155, *B*) and it may occur with explosive force sufficient to scatter the spores.

Formation of Gametophyte. The spore germinates in a similar way to a pollen-grain. Under suitable conditions of warmth, moisture and oxygen-supply, the exosporium is ruptured and the endosporium protrudes to form a short tube. From this a colourless projection (**rhizoid**) passes downwards and attaches the germinating spore to the ground. The cell then begins to divide and a filament is formed, division afterwards taking place in two directions so that a plate of cells (Fig. 157, *A*) is formed. Eventually some growth takes place in three directions and a cushion of cells is formed. The little plant (**prothallus**) which is produced, is usually less in size than a sixpence, and some of the cells on its lower surface grow out into long colourless or brown, unseptate rhizoids which attach it to the soil (Fig. 157, *r*). Owing to the quick growth of the young cells the growing-point lies in a dip and the prothallus becomes heart-shaped. Except at the cushion just below the growing point, the prothallus is one cell thick, and as the cells contain chloroplasts and as some of them produce rhizoids on the under surface, is autophytic or able to obtain its own food from the soil and air. On the cushion, bodies containing egg-cells are produced whilst bodies containing male gametes are formed amongst the rhizoids or towards the rounded margin of the prothallus. These gamete-bearing organs are known as **gametangia**, the

female being **archegonia** and the male **antheridia** (Fig. 157).

A ripe antheridium (Fig. 157, *B*) contains a number of small cells (spermatozoid mother-cells or **spermatocytes**), each of which contains a coiled-up male gamete (**spermatozoid**). The wall-cells surrounding these become distended with water, the apical one is pushed off and the spermatocytes are liberated (Fig. 157, *C*). The spermatozoid (Fig. 157, *D*)

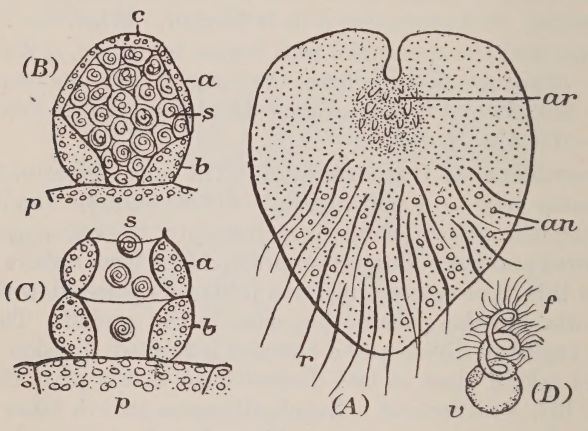

FIG. 157.—Gametophyte of the Fern.

A, diagrammatic representation of prothallus (enlarged). *B*, antheridium in vertical section (× 350). *C*, open antheridium. *D*, spermatozoid (× 600). *a*, annular wall cell; *ar*, archegonium; *an*, antheridium; *b*, basal annular cell; *c*, discoid cap-cell; *f*, cilia; *p*, cells of prothallus containing chloroplasts and protoplasm (dotted); *r*, rhizoids; *s*, spermatocytes; *v*, vesicle.

emerges from its mother-cell as a spirally coiled body with a vesicle (the unused remnants of the mother-cell) at one end and a number of fine protoplasmic projections (**cilia**) at the other. It consists chiefly of nucleoplasm and by the lashings of its cilia is able to move freely through water.

The archegonium (Fig. 160, *D*) is a bottle-shaped organ, produces an egg-cell (oosphere) in the swollen portion (**venter**) sunk in the tissue of the cushion, whilst the canal of the projecting neck is filled with protoplasm (neck canal-cell) containing several nuclei. Between the neck canal-cell and

the oosphere another cell (ventral canal-cell) is formed. The neck canal-cell is enclosed by four longitudinal rows of wall-cells, but, as the venter is sunk in the tissue of the prothallus, there is no need for definite wall-cells to be formed round the oosphere.

Fertilization. When the oosphere is ready for fertilization the canal-cells become disorganized, a mucilage containing a slight amount of malic acid is formed and this oozes out at the top of the ruptured neck, spermatozoids are attracted and cluster round it. Finally one of the spermatozoids forces its way down the neck, fuses with the oosphere and a cell-wall is formed round the egg. As the antheridia are usually

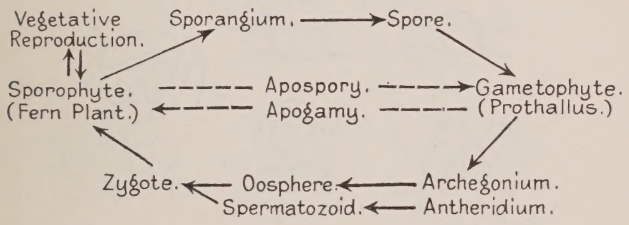

Fig. 158.—Life Cycle of Fern.

ripe before the archegonia there is a probability of cross fertilization occurring.

The egg begins to grow and lives at first on the material derived from the prothallus, but eventually forms its own roots and leaves and becomes the self-feeding plant which we usually consider as the fern-plant.

Alternation of Generations. The life-history of the fern shows two distinct plants, the larger one or ordinary fern-plant which produces the spores and is called the sporophyte or asexual generation, and the small prothallus which produces the gametes and is therefore styled the gametophyte or sexual generation. The spore does not directly give rise to a sporophyte nor does the egg develop into a gametophyte; the two generations alternate with each other. The general life cycle of the fern is represented in Fig. 158.

Development of Sporangium. Each sporangium is a club-shaped body, with a swollen head portion (Fig. 154, *B*). The lower part is the stalk and a small, stalked, lubricating gland (Fig. 156, *g*) is often present on it. The pear-shaped head, when mature, contains a quantity of fine dust similar to the pollen grains of the flowering plant. Each of these particles of dust is a spore (Fig. 154, *C*) and is able to germinate when the surrounding conditions are suitable. Each sporangium arises by the division of a single cell on the placenta into two cells (Fig. 159). The basal cell takes no further part in the production of the sporangium whilst the apical one continues

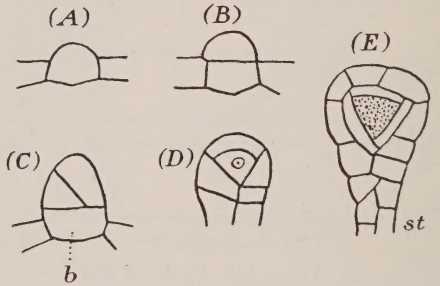

FIG. 159.—Successive Stages in the Development of Sporangium.

In *D*, the nucleus is indicated in the apical cell which gives rise to archesporium and tapetum. In *E*, the archesporium is dotted. The three cells shown round it give rise to tapetum. *b*, basal cell; *st*, stalk.

its division. The lower cells form the sporangial stalk and the upper ones develop into the actual spore-case (capsule). The outer cells of the capsule give rise to the wall-cells, a single tetrahedral cell (archesporium) in the middle divides to form spores, and intermediate cells form the tapetum. The archesporium divides till about sixteen spore mother-cells are formed and then each of these by free-cell division produces four spores, each of which has two coats, an inner delicate endosporium and an outer thicker exosporium. Then disorganization of the tapetal cells, and of other material not used up in the development of the spores, occurs and the spores lie freely in the cavity of the sporangium.

Development of Gametangia. The antheridium arises as a swelling of a cell (Fig. 160) and in its young state can scarcely be distinguished from a young rhizoid. The papilla is separated from the prothallial cell by a wall and then further divisions occur so that wall-cells and a central cell are formed. The wall-cells are three in number, the two lower are ring shaped and the upper cap-cell is discoid (Fig. 160, *B*). The central cell divides into a number of spermatocytes, each of which contains a coiled-up spermatozoid (157, *B*). The archegonium is also formed from a single

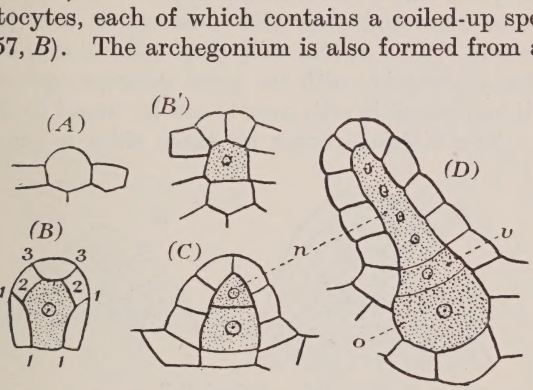

FIG. 160.—Development of Gametangia.

A, *B*, development of antheridium of fern. 1, 2, 3, walls in order of development. The cell which gives rise to spermatocytes is dotted and its nucleus is shown. *A*, *B'*, *C*, *D*, development of archegonium. Cells which give rise to oosphere (*o*), ventral canal-cell (*v*) and neck canal-cell (*n*) are dotted.

superficial cell (Fig. 160, *A*). Division occurs so that a central cell is surmounted by the four primary wall-cells of the neck (Fig. 160, *B'*). As the neck differentiates further, the central cell pushes its way up and forms the neck canal-cell (Fig, 160, *C*) ; then a ventral canal-cell is cut off and the remaining portion is the oosphere (Fig. 160, *D*).

Development of Embryo. The egg or zygote divides by three walls at right angles to each other to form eight cells or octants. One of these octants is the initial cell of the stem and the octant diagonally opposite is the initial cell of the root. Other octants give rise to the foot which absorbs nourishment from the prothallus and a first leaf or

cotyledon. Further cell division and differentiation occurs, new leaves appear, the foot and the primary root gradually disappear, and the rhizome with adventitious roots is formed. Adventitious roots are often formed on the persistent leaf-bases and in an old fern are mainly found there.

The Growing Point. The apices of the roots and stems, as in flowering plants, are occupied by meristem. In the flowering plant the meristematic cells are about the same size, but in ferns and their allies one cell is usually larger than the rest. This **apical cell** (Fig. 161) is shaped something like a pyramid, with its point directed inwards, and the small meristematic cells near it can be traced to divisions from it. The divisions occur on three sides in succession,

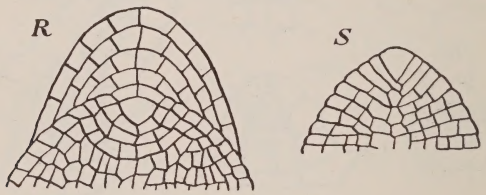

FIG. 161.—Apical Cell.

Diagrammatic L.S. of apices of root and stem. *R*, root with cells of root-cap above the large apical cell. *S*, stem with large apical cell at the actual apex.

and after each segment is cut off, the apical cell enlarges to its original size. Such a cell is said to be three-sided, though it must be noted that this does not mean that there are only three sides to it, but that segments are cut off from three of its sides. This method of division from an apical cell also occurs in the development of the leaf, sporangium, prothallus, foot and cotyledon, though the apical cell is sometimes two-sided only. In the rhizome there are no segments cut off the dome-shaped wall of the inverted pyramid and the apical cell is really at the apex (Fig. 161, *S*), whereas in the root, segments are cut off parallel to the curved wall, and the apical cell is covered by a root-cap (Fig. 161, *R*). The small-celled meristem derived from the divisions of the apical cell develop into the epidermal, cortical and vascular tissues

in a somewhat similar way as in the dicotyledon, though the details are different.

Microscopic Structure of Root. The root has an internal structure similar to that of a dicotyledonous root with two groups of vascular bundles. The protoxylem, however, does not extend to the pericycle and therefore the phloem forms a complete ring round the xylem (Fig. 162). A simple stele with this concentric arrangement of the phloem

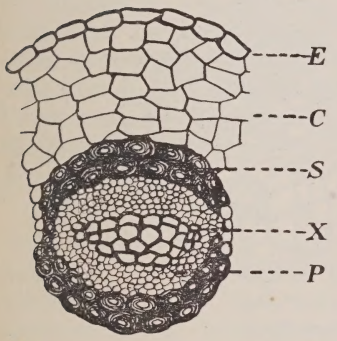

FIG. 162.—T.S. of Root of Hart's-tongue Fern (× 175).

E, epiblema; *C*, cortex; *P*, phloem; *S*, sclerenchyma (endodermis and pericycle); *X*, protoxylem.

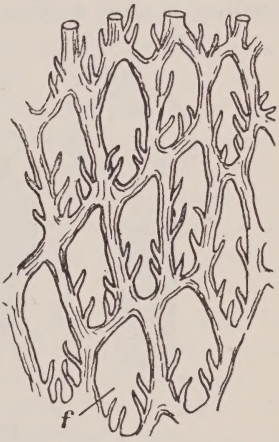

FIG. 163.—Portion of the Vascular Tissue of the Fern shown dissected out.

The larger strands are the main ones of the stem. The smaller strands pass out into the leaves. *f*, foliar gap.

around the xylem, is known as a **protostele,** since it is one of the most primitive kinds of stele. The inner cortical cells often become sclerenchymatous, and lateral roots are developed from endodermal cells, and not from the pericycle as in flowering plants.

Microscopic Structure of Stem. The rhizome has a ring of concentric bundles towards the centre, with some smaller bundles (**leaf-traces**) passing out to the leaf. We

can scarcely speak of cortex and medulla as there are so many bundles scattered about, and so the intervening tissue is often called ground-tissue. Its cells are chiefly parenchyma, but some sclerenchyma is developed in the hypodermal region. The bundles of the ring fuse in a regular way so as to form a diagonal meshwork (Fig. 163) surrounding the central "pith." The leaf-bases occupy the positions outside these diagonal meshes and the latter are therefore called **foliar gaps** (Fig. 163). The concentric bundle may be studied by examining a cross section of a petiole (Fig. 164). Five to

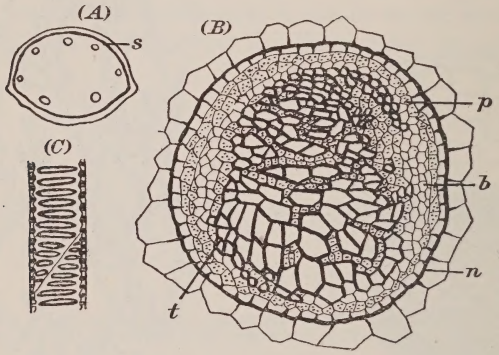

FIG. 164.—Fern Stem.

A, T.S. of petiole of male fern (*Lastrea filix-mas*) (× 4). 3–7 (5 shown) "bundles" towards dorsal, 2 towards ventral surface. *s*, ring of sclerenchyma; *B*, T.S. of "concentric bundle" (× 100). The thickening from endodermis (*n*) extends to the radial walls of cortical cells. Wood-parenchyma and pericycle (*p*) dotted. Phloem (*b*) thin-walled and clear; tracheids (*t*) thick-walled. *C*, scalariform tracheid in longitudinal view.

nine bundles are often present in the ground tissue, two on the ventral and three to seven smaller ones on the more convex dorsal surface. Endodermis and pericycle surround the phloem which, in turn, surrounds the xylem. The phloem has sieve-tubes but these are long, narrow, pointed cells and the sieve plates are on their lateral walls. Phloem-parenchyma is present but there are no companion-cells. The xylem has no true vessels and is therefore much less efficient as a water-conducting cylinder than in the flowering plant. The

tracheids are long cells with pointed ends and are thickened so as to leave narrowly-elliptical pits. As these pits are arranged transversely, a ladder-like appearance is shown (Fig. 164, *C*), and the tracheid is termed **scalariform** (scalaris, a ladder). One or more groups of protoxylem are present and contain spiral tracheids.

The concentric bundle was formerly considered to correspond to a stele and the fern stem was said to be **polystelic.** As the " bundle " may contain two or three protoxylem groups it is best regarded as a **meristele,** and as these meristeles join to form a network the stem is said to be **dictyostelic.**

Microscopic Structure of Leaf. The leaf (Fig. 156) has its mesophyll less differentiated than in the more highly developed flowering plants. The palisade parenchyma is often little different to the spongy mesophyll, the epidermal cells contain chloroplasts and the stomata are always on the lower surface. The internal structure of the leaf in some shade-loving spermophytes approaches the primitiveness shown in the fern-leaf.

British Ferns. Male fern, lady fern, shield fern, hard fern, bracken, parsley fern, scaly fern, filmy fern, maiden-hair fern, wall-rue spleenwort, maiden-hair spleenwort, sea spleenwort, black spleenwort, marsh fern, bladder fern, moonwort (Fig. 155), flowering fern, beech fern, oak fern, limestone polypody, common polypody, hart's tongue, adder's tongue, and a few others which are rare or have no common names.

The hart's tongue (Fig. 42) and adder's tongue have simple leaf-blades, the common polypody has its leaves pinnatifid; all the others have compound leaves. The bracken (*Pteris*) has an aerial stem, grows in drier places than most ferns, and its sori have no indusia as the recurved margin of the leaf serves the same purpose. The hard fern has dissimilar barren and fertile fronds and the sori have no indusia. Indusia are absent also in the maiden-hair, polypody, beech fern, and oak fern. In the royal or flowering fern, the upper parts of the frond simulate an inflorescence, whilst in the parsley fern the reproductive leaves (**sporophylls**) differ

from the vegetative ones as in the hard fern. The scaly fern or rusty-back has the under surface of its fronds covered with chaffy scales. Adder's tongue and moonwort (Fig. 155) differ in so many details from other ferns that they are placed in a separate order. In both these ferns the leaf has a fertile and barren portion, indusia are absent and an annulus is not produced.

Classification. The ferns belong to the phylum Pteridophyta or Vascular Cryptograms (see p. 183). This phylum is divided into several classes, and the class to which the ferns belong is Filicineæ. Nearly all our British ferns have only one kind of spore and are said to be **homosporous.** The foreign water-ferns (*Marsilia, Salvinia, Azolla*) and our native *Pilularia* are **heterosporous.** They produce two kinds of spores; the larger ones or megaspores develop prothalli which bear archegonia whilst the microspores develop prothalli which bear antheridia. *Salvinia* is exceptional amongst ferns because the prefoliation is not circinate. The class Equisetinæ contains the horsetails with jointed stems and cone-like groups of sporophylls (spore-bearing leaves). All living representatives of this class are homosporous. The club-mosses constitute the class Lycopodinæ. The British members of this class have simple leaves which are usually small and moss-like. *Lycopodium* is homosporous whilst *Selaginella* and *Isoetes* are heterosporous.

Pteridosperms. Some extinct relatives of the ferns were trees, had secondary thickening and produced seed-like bodies. These fossil fern-like plants constitute the class Pteridospermeæ.

Homospory and Heterospory. Homosporous Pteridophytes have prothalli which may bear both antheridia and archegonia. In Filices, the order to which nearly all our British ferns belong, the prothalli are often potentially dicœcious, as the antheridia are ripe before the archegonia. In *Equisetum* only one kind of spore is produced but the prothalli are usually dicœcious, the male prothallus being smaller than the female. The formation of two prothalli renders cross-fertilization much more probable as the two

spores may have come from different sporophytes. Heterospory carries the differentiation between the male and female bodies a step further back. The male prothallus is responsible for the production of minute spermatozoids, whereas the female must not only produce the larger egg-cell, but is also responsible for feeding the embryo of the sporophyte during its early stages. The male prothallus is smaller than the female prothallus in *Equisetum*, though both are produced from similar spores. In *Selaginella*, which may be taken as an example of a heterosporous plant, reduction occurs to such an extent that the male prothallus merely consists of one vegetative cell and an antheridium. The microspore, from which the male prothallus is produced, is relatively very small as compared with the megaspore.

CHAPTER XXVII

GYMNOSPERMS—HOMOLOGIES IN SPERMOPHYTA AND PTERIDOPHYTA

Several references have already been made to this group of flowering plants in which the ovule is not enclosed in an ovary and which consequently has a seed without a fruit-wall round it. They are a lower and much older group than the Angiosperms, and a consideration of their characters has been postponed until the fern group had been studied. They are in some respects intermediate between Pteridophytes and Angiosperms, and some of the characters they exhibit are much better understood when they can be compared with similar characters shown by Pteridophytes. This must not be taken to mean that Angiosperms have been derived from Pteridophytes *via* Gymnosperms. The latter appear to have evolved as a side line and are not on the direct route of evolution from a fern to a dicotyledon.

Gymnosperms

Type. The Gymnosperms show a great amount of variability in some things and there is no plant which can be taken as a perfect type of the group. The Scotch fir (*Pinus sylvestris*) is such a well-known British plant that it is usually taken as an example of the Gymnosperms, but it has a number of characters peculiar to itself.

General Characters. Pinus is represented by a number of species which occur in the British Isles though the only one which is native is *P. sylvestris*. This is a lofty tree with a straight main stem, symmetrical branching and red bark. The bark peels off in scales owing to the formation of the

cork in oblique layers instead of in rings as in most trees. Its needle-like foliage (Fig. 165) often has a pale glaucous hue which is perhaps more apparent in situations near the sea than in more inland localities. Its roots have a firm hold on the soil but the ultimate ones have few root-hairs, absorption being effected by the agency of mycorhizæ. On examining the tree in April or May, four kinds of cones may be found on it, one kind which sheds a cloud of pollen when the branch is shaken, and therefore is a staminate one, and three others which are fertile. The oldest and largest fertile cones have their scales wide open, are in their third year at least, and the seeds may have been shed; the medium-sized ones are in their second year and have their scales closely packed together so that presumably the seeds are not ready for dispersion, whilst the smaller ones are in various stages of the first year. Owing to the flowers being borne on cones this particular order of Gymnosperms is called Coniferæ and includes our native yew and juniper as well as many planted trees such as the spruce, cedar, cypress, monkey puzzle and larch, all, except the last, being evergreens.

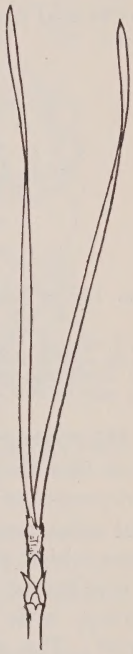

Fig. 165.—Bifoliar Spur of Pine.

A shoot of limited growth with scaly basal leaves and two apical green acicular leaves. The basal portions are somewhat exaggerated.

When we examine a pine branch we find that there are two kinds of leaves (Fig. 165). The main axis is a shoot of unlimited growth, its terminal bud providing for its continuation. On it, little brown scale leaves are present, and in the axils of these, shoots of limited growth develop, each of which stops growing after the production of the needle-like leaves. In the Scots pine the shoots of limited growth produce two needles only and are often referred to as **bifoliar**

spurs, but in some species of Pinus the dwarf shoots have three or five needles. The spurs exist for three or more years and so the tree is an evergreen, but eventually they drop off and the ground in an undisturbed pine-wood is thickly carpeted with the dead spurs. This process, in which the shoots and not the leaves fall off, is known as **cladoptosis.**

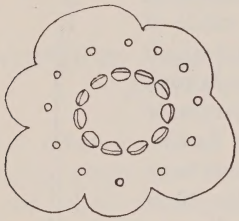

FIG. 166.—General Structure of Pine Stem.

T.S. of young stem of *Pinus sylvestris* showing six bases of scaly leaves, twelve resin canals and eleven fibro-vascular bundles with medullary rays between them (× 10).

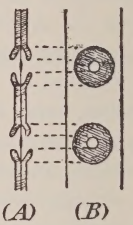

FIG. 167.—Bordered Pits of Pine.

A, tangential view. *B*, radial view. Projections indicate the relationship between the two views of the pit.

Microscopic Structure of Stem. This shows a general plan like that of the dicotyledon (Fig. 166) but there are differences of detail. The medullary rays are very narrow, and secondary growth begins very early so that, except in a stem which is quite young, the fibro-vascular bundles form a continuous ring. Large resin-passages are present in the cortex, with smaller ones in the primary and secondary wood. The xylem has no true vessels or wood-parenchyma, consisting almost entirely of tracheids in which bordered pits are well shown (Fig. 167). Spiral tracheids are present in the protoxylem only. The phloem has no companion cells and the sieve-tubes are prosenchymatous cells with the sieve-plates on their lateral walls. The medullary rays are more complex than those of dicotyledons. Those near the xylem allow for the radial passage of water and compensate for the lack of wood parenchyma, whilst those near the phloem contain starch and proteid material and act in place of companion-cells. Secondary thickening occurs in a similar way as in a dicotyledon (Fig. 101).

Microscopic Structure of Leaf. The acicular leaf is almost semicircular in section and shows a number of xerophytic characters. Its exposed surface is small in relation to its bulk, the epidermal cells are thick-walled and have a strong cuticle, the stomata are sunk (Fig. 168), the hypodermis is sclerenchymatous, and the intercellular spaces are absent or very small, except those beneath the stomata. The meso-

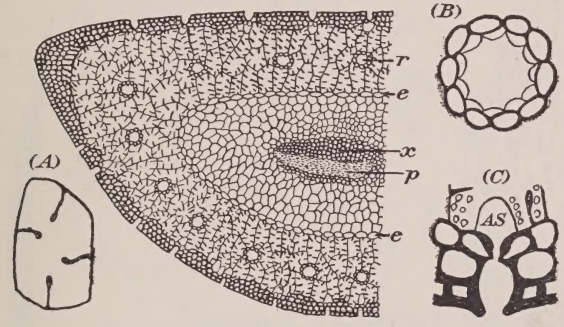

FIG. 168.—T.S. of Pine Leaf (× 35).

r, resin passage; *e*, endodermis; *x*, xylem; *p*, phloem. *A*, mesophyll cell with peg-like projections (× 200). *B*, resin canal with epithelial cells lining it (× 200). *C*, stoma. *AS*, air-space; the guard cells are between the air-space and the stomatal pit (× 200).

phyll never forms a palisade parenchyma on the outer sides but its cell-walls produce a number of peg-like projections (Fig. 168, *A*), which increase the surface over which absorption and excretion can occur.

Staminate Inflorescence. The staminate cone (Fig. 169, *A*) is produced like a branch of unlimited growth. In the axils of the lower scales staminate flowers are formed whilst in the axils of the scales at the top of the cone ordinary bifoliar spurs develop. The staminate flower (Fig. 169, *B*) is therefore homologous to a shoot of limited growth. It consists of an elongated thalamus bearing a number of spirally arranged leaves (Fig. 169, *C* and *D*), each of which has two pollen-sacs on its lower surface, and must therefore be a stamen. As there is no filament, the likeness of a stamen to a leaf is much more strongly shown than in

an Angiosperm. The elongated thalamus is also peculiar though a similar elongation occurs in some members of Ranunculaceæ, especially in the mousetail (Fig. 170), in which, however, since the flower is perfect, the upper portion bears the carpels. The pollen-grain has the usual two coats,

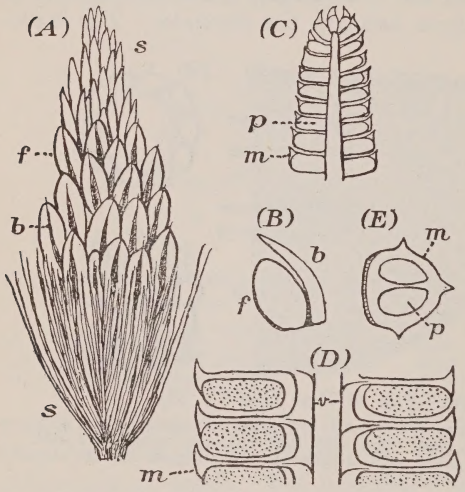

FIG. 169.—Male Flowers of Pine.

A, ♂ inflorescence with shoots of limited growth above and below. In later stages, the axis lengthens so that the flowers are more separated from the bifoliar spurs beneath, whilst the upper spurs open out. *B*, lateral view of ♂ flower (*f*) with bract (*b*). *C* and *D*, L.S. of ♂ flower (× 2 and 7 resp.). Pollen-sacs dotted and vascular bundles (*v*) shown in *D*. *E*, stamen viewed from beneath so as to show two pollen-sacs (microsporangia). *b*, bract; *f*, flower; *m*, microsporophyll; *p*, pollen-sac; *s*, bifoliar spurs.

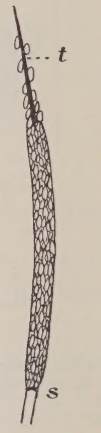

FIG. 170.—Infructescence of Mousetail (*Myosurus minimus*).

Some of the akenes towards the apex have been removed to expose the long thalamus (*t*). The sepals, petals and stamens have fallen off and left a scar (*s*).

exosporium and endosporium, and the former has two lateral inflations or balloons (Fig. 172, *A*) which enable it to be dispersed readily by means of wind.

Pistillate Flower. The pistillate cone (Fig. 171) is usually regarded as a pistillate flower. The thalamus is elongated and bears a number of spirally arranged scales around it. These may be considered as carpels but they do not bear

ovules directly. On the top of each carpel scale a stouter scale is developed (Fig. 171, *p*), and as this bears two ovules, it is called the ovuliferous scale and may be considered as a placenta. At its apex it protrudes out to form a beak termed the **apophysis** (Fig. 171, *ap*). The

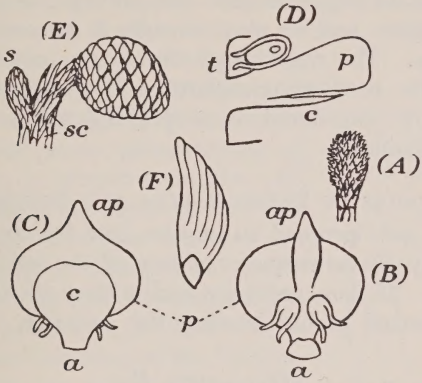

FIG. 171.—Female Flowers of *Pinus sylvestris*.

A, young pistillate cone. *B*, megasporophyll (× 5) showing the two ovules. *C*, megasporophyll, upper (adaxial) side showing carpel scale and ovuliferous scale, with projecting tips of ovule integuments. *D*, section of portion of young cone (× 5). *E*, cone over a year old. The scales (*sc*) on the stem are often withered or broken off. *F*, winged seed (× 1½). *a*, attachment to axis; *ap*, apophysis; *c*, carpel scale; *p*, ovuliferous scale; *s*, shoot of unlimited growth; *t*, position of axis (thalamus).

ovule has one integument and its micropyle is wide and directed towards the thalamus (Fig. 171, *D*).

Formation of Pollen-sac and Ovule. The formation of the pollen-sac is similar to its formation in Angiosperms (p. 165), though the external layer for dehiscence is more like the annulus in the fern than the fibrous layer of the Angiosperm, and there is no transitional epithelium. Tapetal cells and pollen mother-cells are formed and each pollen mother-cell gives rise to four pollen-grains. The formation of microspores in the microsporangium of *Selaginella* goes on in almost exactly the same way. As there is very little difference between the formation of microspores in *Selaginella* and of pollen-grains in the pine, the pollen-sac may then be regarded as a **microsporangium** and the pollen-grains as microspores.

The ovule is formed like that of some Angiosperms, a nucellus arising on the placenta and becoming invested by a single integument. A hypodermal cell divides and tapetal cells are given off. The archesporium forms four potential embryo-sacs but only one of these develops. This tetrad division suggests that the embryo sac-cell is some kind of a spore and we may consider it as corresponding to a megaspore. The nucellus of the ovule may be taken to represent the **megasporangium.** The integument of the ovule may be considered as a special development or as a form of indusium.

Homologies in Pteridophyta and Spermophyta

We must now proceed to inquire how far these ideas are borne out by the subsequent history of the pollen-grain and embryo-sac. If these are spore bodies they should germinate and form sexual plants bearing the gametes. The pollen-

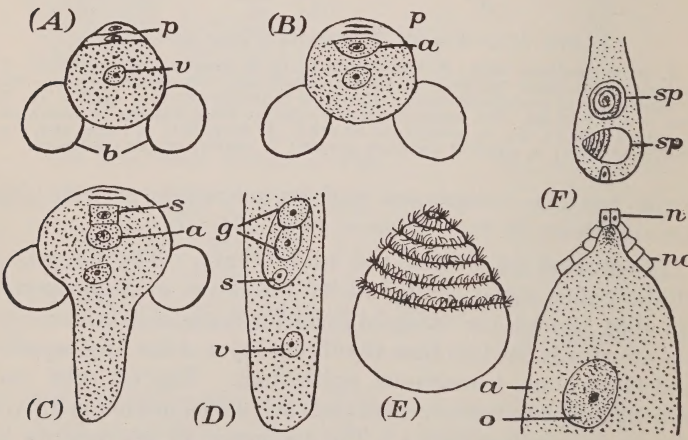

Fig. 172.—Male Gametophyte of Pine.

A, *B*, *C*, *D*, germination of pollen-grain and formation of the generative nuclei; in *D*, only the lower (× 260) portion of the pollen-tube is shown (diagrammatic). *p*, prothallial cells; *v*, nucleus of vegetative cell; *b*, balloon-shaped expansions of the exosporium; *a*, antheridial cell; *s*, stalk or sister cell; *g*, generative nuclei. *E*, spermatozoid of a cycad (Zamia) × about 33. *F*, diagram representing fertilization in a cycad. Only a small portion of the ♀ prothallus is shown. The pollen-tube contains two spermatozoids (*sp*) and is approaching the archegonium (*a*). *n*, neck of archegonium; with canal-cell faintly indicated below; *o*, oosphere; *nc*, a few cells of the surrounding nucellus.

grain, as in an Angiosperm, produces a pollen-tube by means of which the two generative nuclei are carried down towards the oosphere, but this is not all the story. There is an attempt to form a prothallus, two or three small cells being cut off at the opposite end to the pollen-tube (Fig. 172, *p*). There is also an attempt to form a stalked antheridium but only one cell of the stalk is formed. The evidence that the microscopic plant which develops on the stigma of a buttercup, or in the wide micropyle of *Pinus* corresponds to the male gametophyte of Pteridophyta, is almost complete; all that is wanted is the occurrence of cilia on the generative nuclei so that they can swim to the oosphere like spermatozoids. This evidence can also be supplied but not by the Conifers. To obtain it we must go to another group of the Gymnosperms which are called Cycads. In these plants a pollen-tube is formed and by it the male gamete is carried as a generative nucleus nearly to the oosphere (Fig. 172, *F*), then it develops a number of cilia, and by means of these works its way to the oosphere. The ciliated form (Fig. 172, *E*) of male gamete, which accomplishes the final stage of the journey, must therefore be called a spermatozoid.

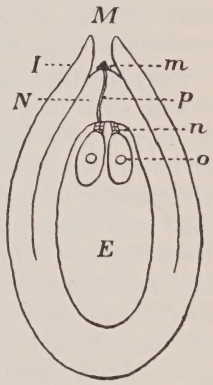

FIG. 173.—L.S. of Pinus Ovule about the Time of Fertilization. (Diagrammatic.)

E, endosperm (prothallus); *I*, integument; *N*, nucellus; *M*, micropyle; *m*, mucilage in which the pollen-grain is caught; *p*, pollen-tube; *n*, neck with ventral canal-cell faintly indicated below; *o*, oosphere.

Female Gametophyte. The embryo-sac should also develop a prothallus and female gametes. The evidence of homology is more definite in this case. The embryo-sac cell (megaspore) divides by free cell-formation and becomes filled with a number of small cells (endosperm). This tissue almost fills up the ovule, displacing the nucellar tissue till only a slight amount (perisperm) is left beneath the wall, and then two or three oval bodies with short necks are formed in it (Fig. 173). The

central cell of each oval body divides into two and, as one of these becomes the egg-cell or oosphere, the other cell must correspond to the ventral canal-cell. The oval body is then an archegonium with a venter, containing an oosphere and ventral canal-cell, and a short neck in which the neck canal-cell has been lost. It is through this neck that the multiciliate spermatozoid of Ginkgo, or of a Cycad, moves to the oosphere (Fig. 172, *F*), most of the previous portion of the journey having been effected as a generative nucleus through the pollen-tube.

Fertilization and Seed-formation. These processes take a long time in *Pinus*. In May the wind-borne pollen-grain is caught by a bead of mucilage in the wide micropyle, and is drawn inwards to the nucellus as the bead dries up. A short pollen-tube is formed but progress is arrested till nearly a year later when the antheridial cell and generative nuclei are formed (Fig. 172). In the meantime the female prothalli and archegonia have been developed in the ovules and the ovuliferous scales (the enlarged apophyses of which form the rhomboidal areas on the exterior of the cone) have grown much larger (Fig. 171). A month or so later fertilization occurs, the cone-scales close up, the egg or oospore develops into an embryo consisting of radicle, plumule and a number of cotyledons. Some of the endosperm is not used up, a little of the nucellar tissue persists as perisperm, and the single integument forms the testa. The seed (Fig. 171, *F*) has a wing which is formed from the placenta at the base of the ovule. When it is blown out of the open scales of the three-year-old cone a spiral twist is given to it and it is consequently carried further by the wind. On germination the radicle forms the tap root, the cotyledons carry the testa above the ground, and the plumule develops. The first year's shoot is a juvenile condition in which no scale leaves or spurs are formed; all the leaves being spirally arranged, green and needle-like.

Recapitulation Theory. During our consideration of the homologies between the reproductive organs in the Pteridophytes and Spermophytes, references were made to many

structures in the latter which are merely rudimentary traces of the structures in the former. In the Pteridophytes, fertilization is effected by means of a motile ♂ gamete (spermatozoid), whereas in the Spermophytes it is nearly always effected by means of a generative nucleus conveyed in the pollen-tube. If the flowering plants have evolved from fern-like ancestors, this change of method has involved many structural alterations. Some structures essential to the method of fertilization adopted by the fern-like ancestor will be unnecessary to the flowering plant, as it has adopted a different method of fertilization. Some of the structures have entirely disappeared in the flowering plants, but relics or traces of others still remain during the development of the sexual organs. In other words, the developmental stages (**ontogeny**) recapitulate some of the structures which were present in the ancestors of the plant. This recapitulation theory also explains many other cases where the "juvenile condition" differs from the mature one. For example, the cotyledons and young leaves of the cleavers are different to the mature leaves (Fig. 9) and may be considered as recapitulations of some phases in the ancestral history (**phylogeny**) of the plant when the leaves were relatively broader than they are in the mature cleavers of to-day. The gorse (Fig. 52, *C*), when mature, has spines, but in the juvenile condition these are absent. The juvenile condition of the gorse may then be considered to recapitulate a stage in the ancestral history of the gorse when spines were absent. It must not, however, be assumed that spineless gorse is an exact copy of the ancestral plant, since modifications may have been induced even in the juvenile condition by evolutionary processes. The juvenile condition of the pine has been referred to above. Many other examples may be given and some traces or relics, which may be recapitulations, have been mentioned on p. 167.

Other Gymnosperms

The yew and juniper are other British members of the order Coniferæ. In the yew the staminate and pistillate flowers are borne on different trees. The stamens bear five to nine

pollen-sacs whilst the pistillate flower, which is scarcely a cone, has a single terminal ovule. A cup-like aril is formed below the integument of the ovule and after fertilization, grows into the sweet, fleshy, red cup investing the green seeds.

Cycads. There are two other orders of Gymnosperms besides Coniferæ. The Cycadinæ include the tropical and

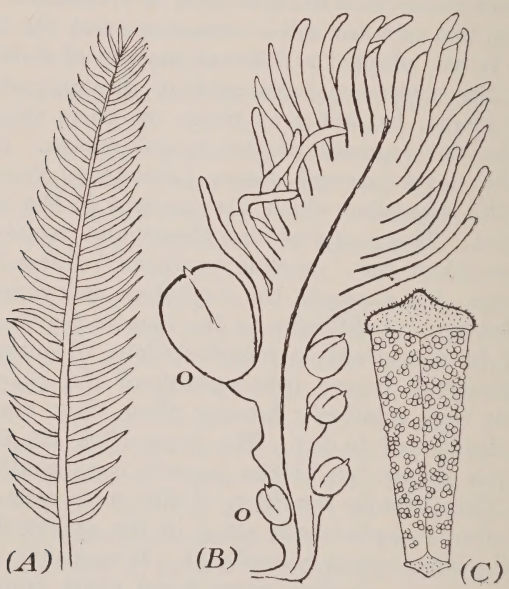

Fig. 174.—Sporophylls of *Cycas*.

A, foliage leaf, × $\frac{1}{12}$ (simplified, after Sachs). *B*, megasporophyll (carpel) × $\frac{1}{4}$. *o*, ovule (megasporangium). *C*, microsporophyll (stamen) × $\frac{1}{4}$, with many microsporangia.

semi-tropical Cycads which are often seen in our "palm-houses." They are diœcious woody plants with large pinnate leaves (Fig. 174). Their reproductive organs must be classed as flowers, since seeds are formed from the ovules, but apart from this character they appear to be more nearly akin to the sporangia of Pteridophyta. In the female plant the fertile leaves (**megasporophylls**) are borne at the summit

of the plant, are smaller than the vegetative leaves and towards the base bear two to eight ovules or megasporangia (Fig. 174, *B*) instead of pinnules. In the male plant the terminal cones consist of numerous **microsporophylls** (Fig. 174, *C*) arranged spirally on the axis. As there are large numbers of microsporangia on the lower surface the correspondence to the sporophylls (fertile fronds) of the fern is nearer than to the stamens (microsporophylls) of an Angiosperm.

The other order Gnetinæ contain plants which show, in many respects, structures intermediate between Gymnosperms and Angiosperms.

The maiden-hair tree (*Ginkgo*) is sometimes placed with Coniferæ, but as important differences occur and the generative nucleus becomes a spermatozoid it is better placed in an order of its own.

CHAPTER XXVIII

MOSSES AND LIVERWORTS

The phylum Bryophyta contains the lowly organized plants known as mosses and liverworts. In many respects the mosses are similar to the liverworts and are therefore grouped with them. Many people do not realize that there are a large number of different kinds of these plants, and it

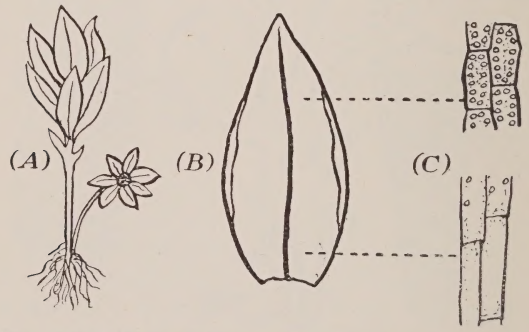

FIG. 175.—Gametophyte of *Funaria hygrometrica*.

A, plant with archegonial shoot, antheridial shoot with rosette of leaves surrounding a group of antheridia, and rhizoids. Length of stem exaggerated (× 3). *B*, leaf with midrib (× 10). *C*, cells from upper and basal portions of leaf, showing chloroplasts (× 100).

surprises them when they learn that there are over 600 species of British mosses and more than 250 species of British liverworts.

MOSSES

Funaria as Type. A moss known as *Funaria hygrometrica* (Fig. 175) is usually taken as a type of Muscineæ,

as the class of mosses is often called. It is chosen as a type because it is a fairly average example of a moss, but more especially because it is a common and well-distributed plant and can nearly always be found with reproductive bodies. It occurs on walls, is frequent on the soil of pots in greenhouses, and has a special liking for cinders or other substratum where burning has occurred. It is the commonest species of the genus *Funaria*, the other four British species of this genus being much rarer.

General Characters. The whole plant (Fig. 175, *A*) is usually less than half-an-inch high and has no root to fix it

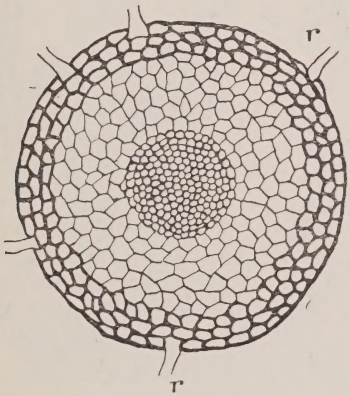

FIG. 176.—T.S. of Stem of *Funaria hygrometrica* (× 66).
r, rhizoid.

to the ground or to obtain nourishment. These purposes are mainly performed by brownish rhizoids which develop from the base of the stem, though, as will be noticed later on, the stem and leaves have such a simple structure, that water can be absorbed by their surfaces. The stem is simple or little branched and bears many imbricated leaves crowded together, especially towards the apex. Corresponding to the small requirements of the plant its microscopic structure (Fig. 176) is simple. There is an outer layer somewhat analogous to the epidermis of higher-organized plants, a many-

layered cortical region with the hypodermal cells thick-walled, and a conducting strand of narrower and longer cells in the centre. This central strand acts as a strengthening core to the stem and, as its cells are elongated, water is able to pass through it more readily than through the cells of the cortical region. It may therefore be considered as a primitive kind of vascular cylinder.

Leaf and Cells. The leaf (Fig. 175, *B*) is broadly ovoid, concave and shortly pointed. It is a simple plate of cells,

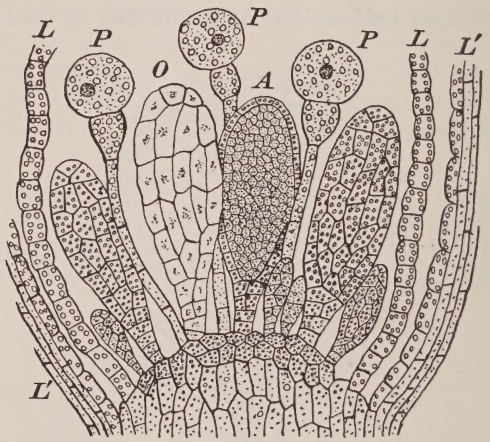

Fig. 177.—L.S. of Apex of an Antheridial Shoot of *F. hygrometrica* (× 250).

Somewhat diagrammatic as when fully mature the shoot is more spread out. The antheridia are shown in different stages of development, one (*A*) is represented in optical section and as showing spermatocytes, one (*O*) is old and empty. Three paraphyses (*P*) and four leaves (*L*) are shown; in *L'* the section passes through the midrib of a leaf.

except at the midrib, which consists of several layers of narrower cells (Fig. 177 *L'*) similar to those found in the conducting strand of the stem. The chief use of the midrib seems to be a strengthening one, though the longitudinal passage of water may be assisted. The cells in the single-layered portion of the leaf contain many chloroplasts and are concerned with photosynthesis (Fig. 175, *C*). The cells in

the basal portion (Fig. 175, *C*) of the leaf are longer and, as may be expected, contain fewer chloroplasts than the more exposed cells in the upper part. No stomata are necessary either for the leaf or stem.

Antheridial Shoot. There are usually at least two different shoots (Fig. 175) attached together to form the rhizome-portion common to both. The larger one is more erect and its upper leaves are more imbricated. The smaller one usually appears to be developed as a lateral branch of the larger one and its upper leaves spread out to form a rosette, in the centre of which a reddish disc of club-shaped antheridia are found. Each antheridium (Fig. 177, *A*) has a short stalk, a wall of a single layer of chlorophyllous cells, and a central mass of spermatozoid mother - cells (spermatocytes). Interspersed with the antheridia are short filaments of three or more cells, the apical cells being very much swollen and almost globular. These filaments or paraphyses (Fig. 177, *P*), as they are called, help to space the antheridia, and as they contain chloroplasts, assist in the manufacture of starch which may be used for the development of the spermatocytes. When the antheridium is ripe, its apex is ruptured, the walls of the spermatocytes become disorganized, and a mucilaginous mass oozes out. The biciliate spermatozoids (Fig. 178, *E*)

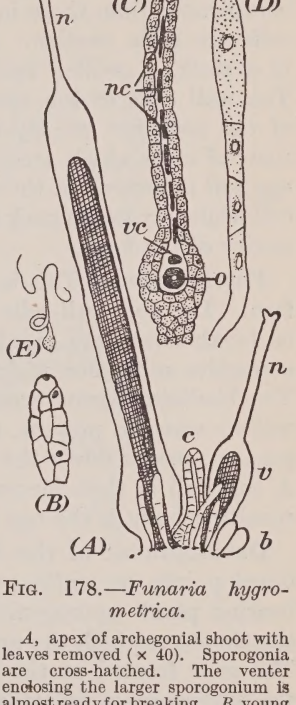

FIG. 178.—*Funaria hygrometrica.*

A, apex of archegonial shoot with leaves removed (× 40). Sporogonia are cross-hatched. The venter enclosing the larger sporogonium is almost ready for breaking. *B*, young archegonium (× 200); *C*, archegonium (after Sachs, × 400). *D*, paraphysis (× 400). *E*, spermatozoid (after Sachs, × 800). *n*, old neck of archegonium; *b*, young archegonium; *v*, enlarged venter; *c*, archegonium; *nc*, neck canal-cells; *vc*, ventral canal-cell; *o*, oosphere.

escape from their mucilaginous investments and are attracted to the archegonia.

Archegonial Shoot. The main shoot (Fig. 175) of the moss plant bears archegonia at its apex. Interspersed with them are **paraphyses** (Fig. 178, *D*), which are much less conspicuous than those in the antheridial shoot, as the upper cells are little swollen. Each mature archegonium consists of a stalk, a swollen venter and a long neck (Fig. 178, *C*). The wall cells of the venter are in two layers whilst those of the neck are one-layered and consist of six longitudinal rows of cells which are somewhat twisted. An oosphere or egg cell is present in the venter, above it is a ventral canal-cell whilst six to ten neck canal-cells are present in the central cavity of the neck.

Fertilization. This is effected in a similar way as in the fern. The top wall-cells (**lid-cells**) of the neck open out or break away, the canal-cells become mucilaginous and an attractive substance, which is probably cane-sugar, is formed. The biciliate spermatozoids swim in the dew, rain, or other watery material present, one of them enters the open archegonium, passes down the neck and fuses with the oosphere. A cell-wall is then formed round the fused bodies and the resulting body is the egg or zygote.

Development of the Sporogonium. The egg does not develop into an ordinary moss-plant but forms a capsule-bearing plant (sporogonium) which is never separated from the shoot on which the archegonium was borne (Figs. 178-9). The cells formed at the base constitute the foot by which the sporogonium is attached to the archegonial shoot, the upper cells give rise to a pear-shaped capsule whilst intermediate cells produce a stalk or seta. During this growth the young sporogonium is still enveloped by the venter (Fig. 179, *A*), the cells of which increase in size so as to keep pace with the growing sporogonium. Finally a limit is reached to the stretching of the cells of the venter and it is broken across (Fig. 179, *B*). The bottom portion of the old archegonium remains as a membranous sheath (**vaginula**) at the base of the seta, whilst the upper portion forms a bonnet

or **calyptra** (Fig. 179, *c*) at the top of the young capsule. The seta has a similar structure to the stem of the ordinary moss plant.

Capsule of Moss. The mature capsule is a pear-shaped body (Fig. 179, *F*) and provision must be made during its

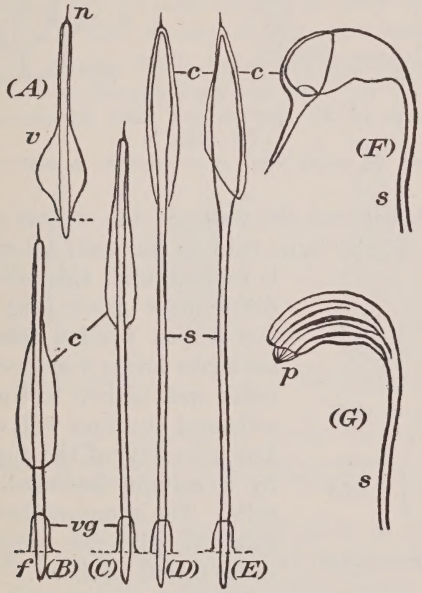

FIG. 179.—Stages in the Development of Capsule of *Funaria hygrometrica* (× 6).

In *A* the sporogonium is still enclosed in the swollen venter. In *B* the venter has broken across. In *D* and *E* the capsule has become swollen. *F*, capsule nearly ripe. *G*, old capsule with lid fallen off. *c*, calyptra; *f*, foot; *n*, old neck; *p*, peristome; *s*, seta; *v*, swollen venter; *vg*, vaginula. Dotted lines represent where the tissue of the gametophyte begins.

development for its nutrition. The conducting strand of the seta is continued into its base and therefore water and inorganic solutions can pass up from the archegonial shoot. Chloroplasts are present in the parenchymatous cells beneath the epidermis and the latter has stomata (Fig. 180). The stomata are usually present in the solid neck (**apophysis**)

or in the lower portion of the capsule. The young capsule can therefore assimilate its own carbonaceous material. Two

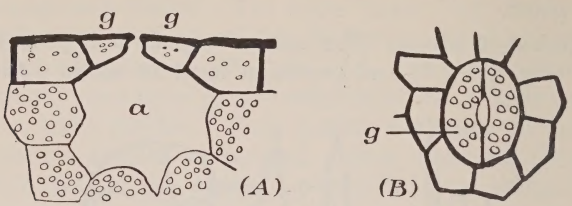

FIG. 180.—Stoma of *F. hygrometrica* from Apophysis of Capsule (× 266).

A, sectional view. *B*, surface view. *a*, air-chamber; *g*, guard-cells with chloroplasts shown.

layers of cells between the wall and the central mass of cells do not grow at the same rate as the rest, a large air-space is formed and this allows for the diffusion of gases (Fig. 181). The cup-shaped portion internal to the air-space forms a spore-sac, with an outer wall of two to three layers of cells and an inner wall of one layer. The concavity of the cup is occupied by a column (columella) of sterile cells. The spore-mother cells in the spore-sac give rise to spores by the usual tetrad division.

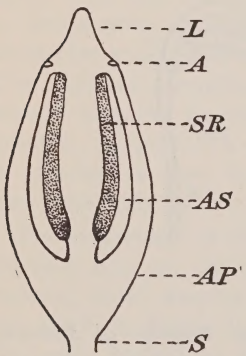

FIG. 181.—L.S. of Capsule of *Orthotrichum anomalum*, var. *saxatile* (× 20).

A, annulus; *AS*, air-space; *AP*, apophysis; *L*, lid (operculum); *S*, seta; *SR*, spore ring.

While the spores are being formed, provision must be made for their dispersal at a time when conditions are suitable. A constriction occurs near the top of the capsule and above the level of the spore cup. The rings (annulus) of epidermal cells in this constriction (Fig. 181, *A*) become differentiated into cuticularized cells, with an intermediate ring of large thin-walled cells. When the capsule is ripe the thick-walled cells interrupt the passage of water and the destruction of the thin-walled cells causes a

lid or **operculum** to separate from the lower spore-containing portion (**theca**) of the capsule. Before this separation is effected a layer of cells beneath the lid is differentiated into a number of tooth-shaped bodies to form a peristome (Fig. 179, *p*). These teeth are hygroscopic, close over the theca during moist conditions so that the spores can only escape when the air is dry. In some mosses (*Bryum* and its allies) the reverse condition occurs as the peristome (Fig. 182) remains closed except when the air is humid. These peristome teeth are developed from the fifth layer of cells from

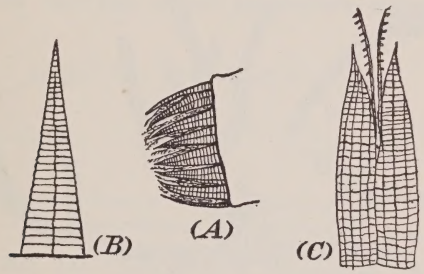

Fig. 182.—Peristome of *Bryum capillare*.

A, top of capsule with lid taken off so as to expose peristome (× 15). *B*, teeth of outer peristome. *C*, two teeth of inner peristome with appendiculate cilia (× 50).

the epidermis. The tangential and parts of the transverse walls of the cells in this layer are thickened, whilst the radial walls remain thin. When ripening occurs the supply of water is cut off from below, and then these unthickened parts of the peristome-layer are broken down and two layers of peristome teeth are present beneath the lid. At the same time the delicate walls of the cells internal to or enclosing the spore-ring are broken down, and then the lower part of the capsule merely consists of the wall enclosing a mass of spores.

Variations of Peristome. In *Funaria hygrometrica* the outer peristome consists of sixteen teeth with a spiral twist whilst the inner peristome has a similar number of shorter and paler-coloured teeth. In *F. templetoni* there is only a single peristome and in several other species of *Funaria* the

peristome is rudimentary or absent. Similar variations in the development of the peristome are shown in other mosses.

Asymmetrical Capsule. The top of the seta is curved, and the ripe capsule therefore has its mouth hanging downwards (Fig. 179, *F* and *G*). As this mouth is in an oblique position a vertical section cuts the capsule into two unequal parts, so it may be preferable to study the structure of the capsule by making sections of a more symmetrical capsule of another

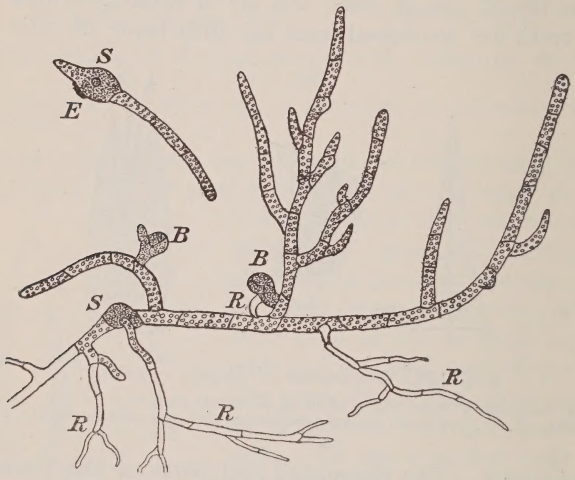

FIG. 183.—Spore and its Germination.

Protonema (after Müller-Thurgau) (× 200). *B*, buds; *E*, portion of ruptured exosporium; *R*, rhizoids; *S*, spore from which development has occurred.

moss, and a *Bryum* (*B. cæspiticium*) common on walls is often used instead of *Funaria*.

Protonema. The spore develops in the usual way by the rupture of the exosporium and the protrusion of the endosporium as a short filament (Fig. 183, left-hand portion), but it does not develop directly into a moss-plant. The filament branches and forms a plant (protonema) which looks like an alga (Fig. 183). Some brown or colourless rhizoids attach it to the soil and the subaerial portions contain chloroplasts. The septa between the constituent cells are usually oblique and

occur just above where a branch is given off. In some mosses (e.g. *Polytrichum aloides*, *Ephemerum* species) the protonema persists for a long time and acts as a means of vegetative propagation, but in *Funaria* and most mosses it is usually much less noticeable. A little bud is formed from a cell near a septum, oblique divisions occur and a three-sided apical cell,[1] which gives rise to the moss-plant, is formed.

Alternation of Generations. As in the fern there are two kinds of plant formed in the life-cycle of the moss (Fig. 184). The ordinary plant is, however, not the sporophyte as in the fern, but the sexual generation or gametophyte

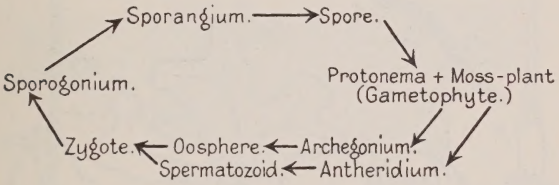

Fig. 184.—Life Cycle of Bryophyte.

and therefore is homologous with the prothallus of the fern. The asexual generation or sporophyte is represented by the semi-parasitic sporogonium.

Liverworts or Hepatics

The life-history of a liverwort is similar to that of the moss, though there are differences in details. Generally speaking, liverworts are plants of wetter habitats than mosses and consequently have a more delicate structure. The gametophyte has much more variation than a moss, whilst the sporophyte displays less.

The liverwort or hepatic perhaps owes its name to the resemblance of one of our common species to the lobes of the liver or hepatic organ. Linked with this resemblance

[1] Growth from an apical cell is usual in bryophytes, but it is not always three-sided; in the sporogonium it is two-sided.

there was probably some idea that the plant was a liver-wort or liver-herb, useful in curing diseases of the liver.

Thalloid and Foliose Liverworts. Besides these simple liverworts in which the vegetative portion is a lobed thallus (Fig. 185, *A* and *C*), there is a larger number with stems

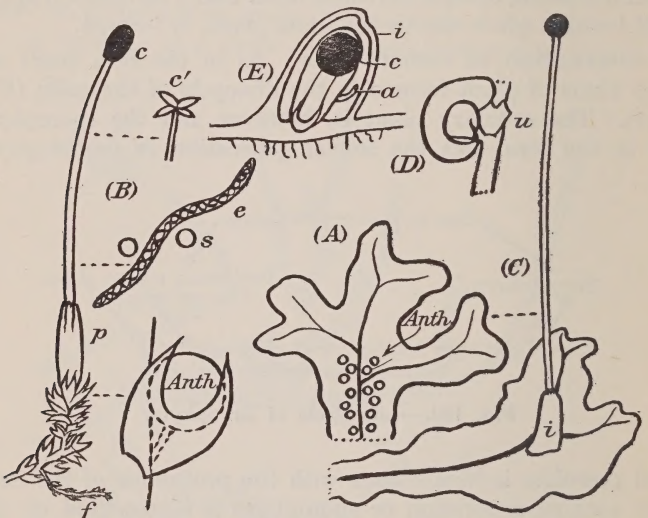

FIG. 185.—Liverworts.

A, *Pellia fabbroniana*, ♂ plants, showing dichotomous branching and antheridia (*Anth*). *B*, *Cephalozia bicuspidata* with leaves, flagellum (*f*), "perianth" (*p*), ripe capsule (*c*), burst capsule (*c'*), elater (*e*), spores (*s*) and antheridium (the unexposed portion indicated by dotted lines). *C*, ♀ plant of *P. fabbroniana* with ripe capsule and involucre (*i*) enclosing calyptra. *D*, two-lobed leaf of *Frullania dilatata* (postical lobe forming a water-sac) and underleaf (*u*). *E*, L.S. of young sporogonium of *P. fabbroniana* enclosed in involucre (*i*) and calyptra (*c*). An old and probably unfertilized archegonium (*a*) is present.

and leaves (Fig. 185, *B*), and these are often considered as mosses by the uninitiated naturalist. The leaves are very variable in shape ; in some Aplozias they are almost orbicular, in Cephalozias (Fig. 185, *B*) they are bilobed, in *Diplophyllum* they consist of two parts pressed together and in *Trichocolea* their branches are so numerous and slender than an algal appearance is presented.

Type. A thalloid liverwort known as *Pellia epiphylla* is often taken as an example. It is fairly typical of the thalloid

liverworts, and if we imagine its lobes to be cut up so as to form leaf-like portions, of the foliose kinds as well.

There are three species of Pellia in the British Isles, and all of them are usually found in wet situations. The commonest one is *P. epiphylla* which has its antheridia and archegonia on the same plant. Another common species in limestone districts is *P. fabbroniana* (Fig. 185, *A* and *C*), whilst the rarer *P. neesiana* is usually found at higher altitudes. The two latter species are dicœcious, i.e. their antheridia and archegonia are on different plants so that we may speak of a male gametophyte or a female gametophyte.

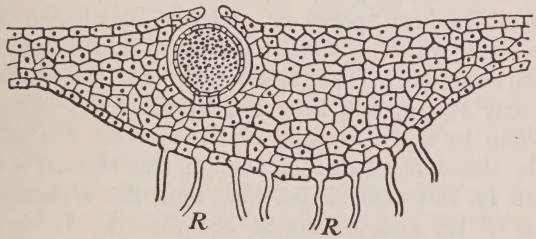

FIG. 186.—*Pellia.*
Section of middle portion of thallus, showing an antheridium (× 50). *R*, rhizoids.

Thallus. The thallus (Fig. 185, *A* and *C*) has a dorsiventral structure, the convex under surface producing unicellular rhizoids, whilst the upper surface is slightly concave and its cells contain more chloroplasts. The branching is dichotomous and there is no true midrib, though the thallus is thicker in the middle (Fig. 186) than at the margins, tapering off from ten to twelve layers to a single one.

Antheridia and Archegonia. The archegonia are initiated at the end of summer on a cushion or receptacle just behind the growing point. The tissue below them grows forward so as to form a protective involucre (Fig. 185, *E*). Before the archegonia are developed, antheridia [1] are formed lower down on the upper surface of the thallus on each side of the "midrib." They are sunk in little pits which are

[1] This refers to the monœcious species, *P. epiphylla.*

arched over by projecting growths of the thallus (Fig. 186). The archegonia and antheridia are similar to those of Funaria, though the antheridia are almost spherical.

Formation of Sporogonium. Fertilization takes place and the sporogonium develops during the winter months. In January or February the sporogonia may be found invested by the calyptra formed from the archegonial wall and by the involucre formed from the thallus. The seta is a short body of small cells, and is surmounted by the globular body of the young capsule (Fig. 185). The peripheral portion (**amphithecium**) of the theca does not develop any air-space, and all the cells of the inner portion (**endothecium**) of the capsule develop either into spores or elaters. The latter are long, slender and brownish cells with a double spiral thickening (Fig. 185, *B*) on their walls. They assist in the nutrition of the spores in the early stages, and later on, by their wriggling movements, help in the dispersion of the spores. No columella of sterile tissue is produced, though the elaters are more abundant in the central portion, and the elaborate contrivances of lid and peristome are absent. During April (often later in the north) the cells of the seta elongate rapidly, the calyptra is ruptured, and the capsule is elevated on a delicate whitish seta which is often several inches long. The top portion of the old venter is not carried upwards on the top of the capsule but the burst venter remains as a sheath round the base of the seta. This sheath is termed the calyptra, though it really corresponds to both the vaginula and calyptra of a moss. The capsule separates into four valves (Fig. 185, *c'*), the spores are liberated and the seta of thin-walled cells shrivels up. The whole process of seta-elongation and spore-dispersal may be accomplished in a few hours, though the processes between fertilization and the ripening of the capsule, occupies over six months.

Germination of Spore. The spores of most liverworts develop similarly to those of a moss but the protonemal stage is of much shorter duration. In Pellia the first divisions of the spore are exceptional, as they occur before the spores are liberated from the capsule.

Foliose Liverworts. A large number of liverworts show differentiation into stem and leaf (Fig. 185, *B* and *D*). The stem is usually creeping and the leaves are arranged alternately on each side of the stem. On the under surface rhizoids, and frequently a third row of leaves (underleaves), are present (Fig. 185, *D*). When underleaves occur they are usually smaller than the lateral ones. The archegonia are developed at the top of the stem and are usually protected by an involucre of modified leaves (Fig. 185, *p*). The antheridia are borne in the axils of leaves which may be similar to the ordinary leaves or modified. They are stalked, spherical bodies (Fig. 185, *Anth*) and may be present on the same plant as the archegonia, or, as is more usually the case, on different plants. In other respects the structure and development of the various organs is similar to what has been described for *Pellia*. Three of the commonest and most widely distributed foliose liverworts of the British Isles are *Lophocolea cuspidata*, *Diplophyllum albicans* and *Cephalozia bicuspidata* (Fig. 185, *B*).

Structure of Marchantia. A group of thalloid liverworts, of which *Marchantia*, *Lunularia* and *Conocephalum* are examples is, in some respects, more highly developed than the groups to which either *Pellia* or the foliose liverworts belong.

The thallus has become differentiated so that a distinct epidermis with pores leading into air chambers (Fig. 188) is formed. On the floor of an air-chamber, little pillars of chlorophyllous cells are present, and these serve as assimilatory tissue. The cells in the lower part of the thallus contain little or no chlorophyll and the under surface bears rhizoids of two kinds, long, unicellular rhizoids of the usual kind, and others (Fig. 187, *R*) with peg-like projections on the inside. Purplish or brownish scales are also present. The archegonia in Marchantia are elevated on a stalk and are borne on the under surfaces of the rays of a star-shaped receptacle (Fig. 187, *a*). The antheridia are borne on a similarly elevated disc with a wavy margin (Fig. 187, *An*). The vegetative differentiation is correlated with the less aquatic habitats of the plants. *Conocephalum* occurs by stream sides and usually above the *Pellia* zone ; *Marchantia* is found in damp rather than

wet situations ; *Lunularia* is frequent on damp pots in greenhouses, whilst some other members (e.g. *Targionia* and

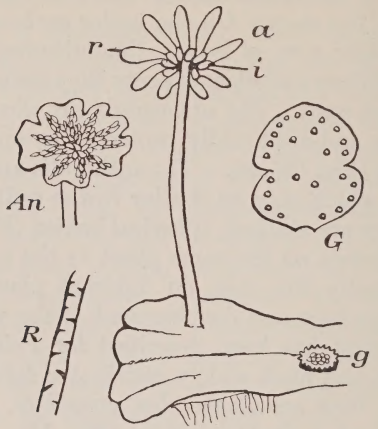

FIG. 187.—*Marchantia polymorpha.*

Thallus with archegoniophore (*a*) showing under surface, with rays (*r*) and intermediate involucres (*i*) enclosing young sporogonia. *g*, gemma-cup (× 1½). *An*, antheridiophore from another plant (× 1½) indicating antheridial pits on surface. *G*, gemma showing oil-cells (× 30). *R*, one kind of rhizoid (× 150) which has projections from the inner walls.

Reboulia) of the family Marchantiaceæ are almost xerophytes. The formation of an elevated archegonia-bearing body **(archegoniophore)** enables the later-developed spores to be dispersed

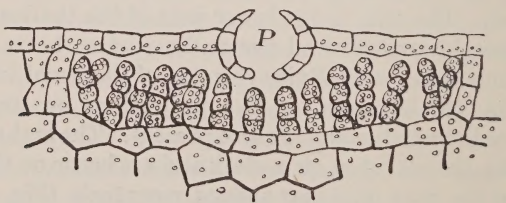

FIG. 188.—Section of Thallus of *Marchantia polymorpha* (× 260).

P, barrel-shaped pore communicating with an air-chamber containing vertical rows of assimilating cells.

and it may be useful in other ways, though in most members of Marchantiaceæ it remains short till after fertilization is

effected. An **antheridiophore** is exceptional and is found in few genera besides *Marchantia*.

General

Vegetative Reproduction in Bryophytes. This does not occur to any great extent in *Funaria*, even by protonemal growth, but in some mosses, branches, leaves or groups of cells (**gemmæ**) may become detached from the parent plant and develop into new moss plants (Fig. 189). In liverworts reproduction by means of gemmæ is common. In the foliose species (Fig. 189, *D* and *E*) the gemmæ consist of few cells

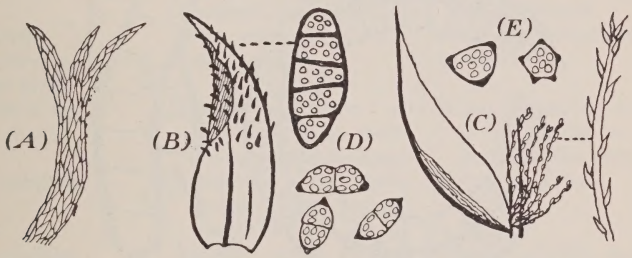

Fig. 189.—Vegetative Reproduction in Bryophytes.

A, *Webera proligera*, gemma from axil of leaf (× 53). *B*, leaf of *Orthotrichum lyellii* with gemmæ. Single gemma containing chloroplasts (× 200). *D*, gemmæ of *Cephalozia bicuspidata* from leaves (× 200). *C*, leaf of *Plagiothecium elegans* with filamentous offshoots (× 10); single offshoot (× 33). *E*, gemma from apex of leaf of *Lophozia ventricosa*. *Webera*, *Orthotrichum* and *Plagiothecium* are mosses; *Cephalozia* and *Lophozia* are liverworts.

and are often detached from the apices of leaves, but in the thalloid *Marchantia* and *Lunularia* they are formed in little cups, and consist of many cells (Fig. 187, *G*). The gemma-cup is ring-shaped in *Marchantia* (Fig. 187, *g*) and half-moon-shaped in *Lunularia*.

Deviations from Types described. The foregoing account of the bryophytes does not take particular account of many mosses and liverworts which depart in some way or other from the structure as described. Some of the more important deviations have been alluded to and a few others are given below. In many mosses the shoots are creeping and much branched and rhizoids may be developed from almost any part, even from leaves. A conducting strand is absent in

some mosses, whereas in *Polytrichum* it consists of two parts bearing some analogy to the xylem and phloem of flowering plants. A midrib is often absent, the leaf being a simple plate of cells. In some other mosses the leaf may be a more complicated structure. In *Polytrichum* assimilating plates of tissue stand up on the upper surface, in *Leucobryum* (Fig. 190, *A*) and *Sphagnum* (Fig. 190, *B*) there are two kinds of cells, some with chlorophyll and others without, and in species of *Tortula* (Fig. 146, *B*) and *Bryum*, the midrib is

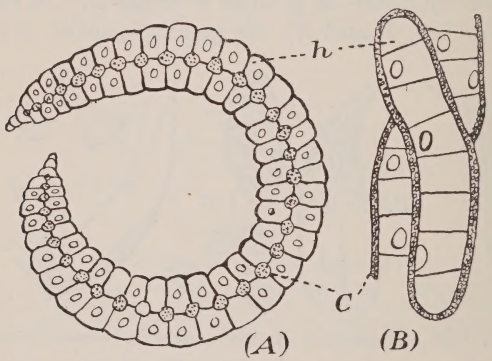

Fig. 190.—Hyaline Cells.

A, section of leaf of the moss *Leucobryum albicans*, which curls up when placed in water (× 80). *B*, a few cells from the leaf of the bog moss, *Sphagnum acutifolium* (× 240) with strengthening fibres and pores in the hyaline cells. *h*, hyaline cells; *C*, cells containing chloroplasts.

often prolonged into a long hair. The antheridia and archegonia in *Hypnum* and its allies are on short lateral branches and the distribution of the two kinds of gametangia is very variable, not only in *Hypnum* but in other mosses as well. Some species like *Funaria hygrometrica* are monœcious, but many other species are diœcious. The seta is sometimes very short or absent, the peristome may be rudimentary or wanting and, in a few species, a lid is not developed.

Anthoceros. In the *Hepaticæ* the most important deviation from the liverworts described is in *Anthoceros*. Each cell of the thallus has one large chloroplast, the sporogonium is a pod-like body and contains a columella. *Riccia* is a reduced derivative from the Marchantiaceæ and its sporogonia are immersed in pits of the thallus.

General Differences between Mosses and Liverworts

	Mosses.	Liverworts.
Vegetative portion.	Stem and leaves.	Sometimes thalloid.
Leaves. . . .	Usually radially arranged.	When present usually seem to be distichous.
Underleaves . .	Absent even in creeping mosses.	Often present and smaller than ordinary leaves.
Leaf-shape . .	Usually more or less ovate or lanceolate, seldom two-lobed.	Very variable, often lobed, sometimes much-divided.
Midrib . . .	Often present.	Absent or indefinite.[1]
Conducting strand of stem.	Often present.	Absent.
Cells of leaf . .	Usually smaller or narrower with thickening evenly disposed.	When thickening occurs it is usually at the angles of the cells.
Protonema . .	Somewhat persistent, occasionally very much so.	Very short-lived.
Antheridia . .	Usually much longer than broad and occur in clusters at the apices of the stem or of its branches.	Usually globose and in leaf-axils or in pits of the thallus.
Archegonia . .	Surrounding leaves seldom much different from ordinary leaves. Stalks usually better developed.	Relatively shorter and often surrounded by an involucre formed from the thallus or from modified leaves.
Neck	Usually twisted.	Usually straight.
Neck canal-cells .	Often more than 10.	4–8.
Capsule and seta.	Strong, long-living structures. Capsule usually opens by a lid.	Fragile and, after maturity, short-lived. Capsule usually 4-valved.
Peristome . .	Usually present.	Absent.
Columella . . .	Present.	Absent except in Anthoceros.
Elaters . . .	Absent.	Nearly always present.

[1] In a few liverworts (e.g., *Diplophyllum albicans*) there is a line of elongated cells up the middle of the leaf.

	Mosses.	Liverworts.
Calyptra . . .	Carried up to the top of the capsule.	Remains at the base.
Neck of caspule .	A solid structure.	Absent.
Stomata . . .	Present in apophysis or on wall of theca.	Absent except in capsule of *Anthoceros*.
Air-chamber . .	Present in amphithecium.	Absent.
Sporogonium . .	Semiparasitic.	Parasitic.
Vegetative reproduction.	Common but gemmæ comparatively rare.	Gemmæ frequent.

CHAPTER XXIX

THALLOPHYTA—ALGÆ

All kinds of plants less highly organized than bryophytes are included in the phylum Thallophyta. It includes the simple, single-celled plants which form a green incrustation on walls or trees, or which are present in water, as well as the complex, many-celled, sea-weeds. In every case the plant-body is not differentiated into stem and leaf, and such a body, whether it is unicellular or multicellular, is known as a **thallus.** Reproduction is effected both by asexual (see p. 300) and sexual methods, but an alternation of generations is seldom shown in a definite way. The ordinary plant is usually either an actual or a potential gametophyte. The male gametangia may sometimes be called antheridia, but they are usually of a much simpler nature than those of the bryophytes. The female gametangium is much more primitive than in the mosses, never has a neck, and is not termed an archegonium, but is usually called an oogonium.

A convenient method, though not a strictly scientific one, of dealing with the thallophytes is to consider them under three groups, algæ, fungi and lichens. An **alga** contains chlorophyll and is able to obtain carbonaceous food from the air. A **fungus** has no chlorophyll and must be either saprophytic or parasitic. A **lichen** is a compound plant consisting of algal cells and fungal filaments living together in symbiotic relationship.

Morphological Differentiation and Physiological Specialization. Since the thalli of the algæ vary from the single-celled structure of Protococcus to the multicellular complex of the sea-weed, they provide a useful series

for the study of differentiation. The primitive blob of protoplasm, from which all organic life evolved, developed on one side into plants with cells having walls of cellulose and containing chloropyll, and on the other side into animals without cellulose or chlorophyll. Probably the primitive alga had no nucleus or cell-wall and all the work of the plant had to be done by the general protoplasm (cytoplasm). A special portion of the protoplasm was differentiated to form a nucleus and the cell was enclosed in a cellulose envelope. This differentiation relieved the cytoplasm of some work in connection with cell-division and protection, but the work of carbon assimilation was still done by the cytoplasm containing chlorophyll diffused through it. The next step may have been the delegation of carbon assimilation to special bits of protoplasm containing the chlorophyll and thus chloroplasts were differentiated. In many of the simple algæ the chloroplasts are large (Fig. 197) compared to the chloroplasts in the higher plants, in fact a single chloroplast often occupies a large part of the cell. This is not a great advance from the state when the chlorophyll was diffused through the cytoplasm. The absorption of light is efficiently done, but the bulkiness of the chloroplasts interferes with their efficiency as starch manufacturers. In such cases, small, denser portions of colourless protoplasm are usually formed on the chloroplast, and these bodies, which are termed **pyrenoids** (Fig. 197), manufacture the starch. As the plant body increased in size and in number of cells, further allotting of the work became possible, and in such an alga as the bladder wrack, several kinds of cells or groups of cells (tissues) were differentiated so as to perform special functions. The correlation between the differentiation of structure and specialization of function in the plant-body may be considered, not only in the algæ but extended to the evolution of the complex plant-body of a flowering plant.

Filamentous, Membranous and Spherical Forms. As the plant-body increases in number of cells there are three main lines of development. The division of the cells may take place in one direction so that a thread or filament is formed.

If division occurs in two directions a flattened plate of cells will be formed, whilst when division occurs in three directions, a solid mass of cells will be produced. If the division is equal in all three directions the plant-body will be spherical, but this seldom takes place (Fig. 195). In most cases growth occurs more in one direction than in another, and consequently the plant-body assumes various shapes. This kind of development allows the cells to be differentiated, some being used for reproductive purposes, whilst others have work connected with feeding, breathing, or protection allotted to them. Difficulties soon arise in regard to the transport of material necessary to the life of the cells. Those on the outside of the thallus are able to obtain what they require, but the inner ones are in danger of starvation or suffocation. The difficulties may be partially overcome if the thallus becomes hollow, but this method involves such a weakening in rigidity that it is rarely followed. Some method for transporting the necessary materials to the inner cells and for giving rigidity to the whole thallus, especially in the case of land plants, must be adopted if success is to be attained. The conducting system is of a very primitive nature in the thallophytes, but in the flowering plants has been elaborated into the highly successful vascular system which has been described previously. These general ideas on differentiation of structure and specialization of function must be borne in mind when we are considering the algæ, especially as these plants are the probable ancestors of most of the other groups of plants.

Protococcus

One of the most abundant and widely-distributed alga is *Protococcus viridis* (= *Pleurococcus vulgaris* of many authors), which forms a green coating on walls and tree-trunks. The use of the microscope reveals that this coating consists of a large number of spheroidal cells (Fig. 191), each of which is surrounded by a strong wall of cellulose, and has a nucleus differentiated from the rest of the protoplasm. The green colour sometimes appears to be due to the diffusion of the chlorophyll through all the cytoplasm, but usually a large lobed chloro-

plast can be distinguished. The method of reproduction is almost entirely a vegetative one. Division occurs in two directions in the same plane and four daughter-cells are formed. The products of these divisions do not separate

Fig. 191.—*Protococcus viridis* (× 650).

The protoplasm is dotted and the chloroplasts are darkened. *A*, plasmolysed cells. *B*, Palmella-like state.

readily from each other and consequently groups of two and four cells are plentiful in our microscopic preparation. It is probable that other methods of reproduction occur, in fact both zoogonidia (p. 300) and isogametes (p. 297) have been recorded, but their formation is rare.

Chlamydomonas

The green coloration of water in a rain-tub or similar habitat is often due to myriads of ovoid or spherical cells of *Chlamydomonas* (Fig. 192). The observation of living

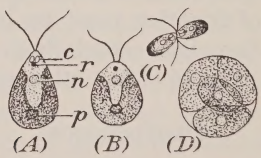

Fig. 192.—*Chlamydomonas* (× 500).

A and *B*, two different species. *C*, gametes conjugating. *D*, four daughter-cells in wall of old mother-cell. *c*, contractile vacuole; *r*, eye-spot; *n*, nucleus; *p*, pyrenoid.

specimens of this unicellular alga, under the microscope, presents greater difficulties than with Protococcus, as they are motile bodies. Through the cellulose wall at the more pointed end two extremely slender projections (cilia) of protoplasm pass, and by their movements propel the cell

through the water. The way in which the propulsion is effected may be compared to that of the arms in breast-swimming ; the backward movement of the arms causes the body to move forward, but the forward movement does not counteract this effect as the arms are brought back by the side of the body. A nucleus is present in the central portion of the protoplasm and surrounding it is a cup-shaped chloroplast, which almost appears to fill the cell. Situated more deeply in the concavity of the cup is a pyrenoid (Fig. 192), whilst the colourless cytoplasm is apparent at the pointed end, which is the anterior one during movement. This hyaline end contains two contractile vacuoles and an orange-coloured pigment-spot (Fig. 192). A **contractile vacuole** is a structure by which waste material and excess of water is excreted. A little space appears in the protoplasm and gradually gets larger till it reaches its full size. Then a sudden collapse occurs and the gradual refilling is repeated.

Animal Characters. The speck of reddened cytoplasm is believed to be concerned with the perception of light.

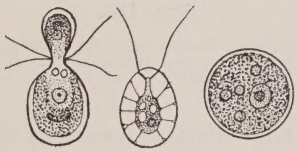

Fig. 193.

A, heterogamy in *Chlamydomonas monadina* (after Goroschankin). *B*, *Sphærella lacustris* (after Schmidle). Four contractile vacuoles and a pyrenoid are present. *C*, resting cell of *Sphærella* (after Wollenweber) (× about 500).

Light of a certain intensity causes organisms containing a pigment spot to move towards it, whereas movements in an opposite direction occur when the light is stronger. Such phototactic movements occur in many unicellular organisms which contain a pigment-spot, and as pigment is present in the eyes of animals, the pigment-spot is often termed an **eye-spot.** Both eye-spot and contractile vacuole are more often found in minute animals than in plants. *Chlamydo-*

monas therefore possesses three kinds of structures, cilia for motility, eye-spot for sensitiveness to light, and contractile vacuole for excretory purposes, which are more frequent in animals than in plants, and it is therefore claimed by some zoologists as a minute animal. Botanists claim *Chlamydomonas* as a plant because it has a cellulose covering and because its possession of a chloroplast enables its method of feeding to be entirely plant-like in character. Its reproductive methods are also more like those of plants.

Vegetative Reproduction. In the common method of reproduction the cilia are drawn in and the cell comes to

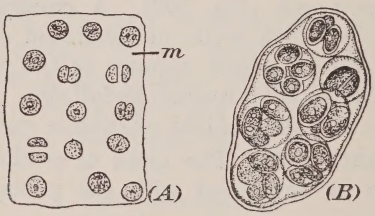

FIG. 194.

A, *Palmella mucosa* from pool, Bruton (probably a state of Tetraspora as indicated by method of division); × 500. *m*, mucous investment. *B*, Palmella state of *Chlamydomonas monadina* (after Goroschankin).

rest. Sooner or later division occurs so that two, four (Fig. 192, *D*) or eight daughter-cells are formed, the successive divisions occurring in three planes at right angles to one another. Each cell develops two cilia and a cell wall and, on the dissolution of the wall of the parent-cell, is liberated as a new *Chlamydomonas* individual. In another vegetative method which is occasionally adopted, the daughter-cells continue to divide and are embedded in a mucilage formed from the walls of the parent-cells and the first-formed daughter-cells. This condition is often known as the **Palmella-state** (Fig. 194, *B*), from its likeness to the ordinary mode of life in an alga called *Palmella* (Fig. 194, *A*). Eventually the cells acquire cilia and cell walls, and escape from the jelly which surrounds and separates them.

Sexual Reproduction. This is effected by motile gametes which are produced in a similar manner to that described for the vegetative division, though the colonies contain a greater number of cells: sixteen, thirty-two or even more being present. As the gametes are equal they are termed **isogametes.** They are smaller than the vegetative cells and are usually without cell-walls. Two gametes come into contact with each other at their anterior ends (Fig. 192, *C*) and gradually fuse together (**conjugate**). The cilia are withdrawn and a thick cell-wall is formed. The resulting egg (**zygospore**) has a resting-period, but eventually it divides into a small number of parts which develop into ordinary individuals. In a few species **heterogamy** (production of two kinds of gametes) has been shown to occur. The gametes are of two sizes (Fig. 193, *A*); the larger gamete (megagamete) contains more food-material and is less active than the smaller gamete (microgamete), so that we may regard the former as the female and the latter as the male sexual cell. There is no alternation of generations, though the resting egg may be regarded as an incipient sporophyte and the products of its division as **zoospores** (motile spores) which immediately form one-celled gametophytes. It is probable that reduction of the chromosomes occurs during this division. The products of the asexual method of division may be considered to be **zoogonidia** (p. 300) which immediately form fresh individuals. The differentiation of sex and the discrimination of a gamete-producing plant from a spore-producing one is very slight.

Sphærella. *Sphærella* (*Hæmatococcus*) is similar to *Chlamydomonas*, its chief points of distinction being the possession of many contractile vacuoles and the intervention of a mucilage between the protoplasm and the cell-wall (Fig. 193, *B*). The resting condition (Fig. 193, *C*) is usually of longer duration and red colouring matter is often present in the protoplasm. Some species are not uncommon in small pools and *S. nivalis* is responsible for the red coloration of snow in arctic regions.

Colonial Forms. It has been noticed that in *Chlamydomonas*, during certain stages, division occurred in three

directions so that a colony of eight to thirty-two or even sixty-four cells was formed, though the cells eventually separated from one another. In some allied plants a similar method of division occurs, the cells do not separate from one another, are embedded in a mass of mucilage and form a colonial condition which is permanent. In *Pandorina* (Fig. 195, *C*) the colony contains about sixteen cells, and as the outer ones are ciliated, the colonial plant is able to move about. In *Eudorina* (Fig. 195, *B*) about thirty-two ciliated cells form a hollow sphere, whilst in *Volvox* (Fig. 195, *A*), the culminating

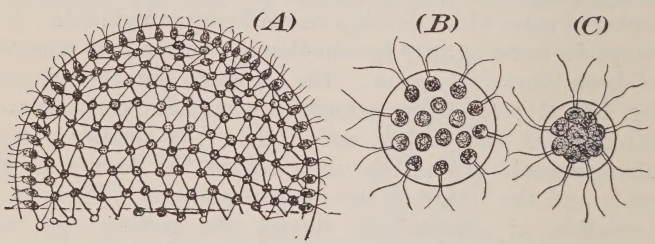

FIG. 195.—Colonial Algæ. All × 150.

A, *Volvox* in vegetative condition (rather more than half of small specimen shown). *B*, *Eudorina elegans*. *C*, *Pandorina morum*.

member of the series, there are more than a thousand ciliated and peripheral cells. Reproduction is effected as in *Chlamydomonas* and the gametes of the series gradually differentiate into male and female till, in *Volvox*, definite spermatozoids and oospheres are formed. *Volvox* represents the utmost development along the line where division is equal in three directions. It is not uncommon in pools, is large enough to be seen by the naked eye, and, owing to its motility, has been claimed by some zoologists as an animal.

ULOTHRIX

The filamentous species of green algæ are very numerous and their main characters may be shown by taking *Ulothrix*, *Spirogyra*, *Vaucheria*, and *Œdogonium* as examples. Some species of these genera are common in ponds and ditches, especially in the spring. The simplest of these is *Ulothrix*,

in which all the cells are separated from one another by septa (Fig. 196). The thallus is unbranched and consists of a large number of short cells, each with a single plate-like chloroplast arranged around a central vacuole. The nucleus is inconspicuous but one or more pyrenoids are easily seen. The end-cell which fixes the plant to the substratum is often colourless and may be regarded as a kind of unicellular rhizoid.

Fragmentation. Reproduction is effected in various ways. A common vegetative method during periods of active growth is that of fragmentation, the filament splitting up into a number of fragments, each of which can develop into a new thread. It is by modified fragments of this kind, in which the cell-walls have been thickened, that most species endure during the winter.

Sexual Reproduction. This is effected by isogametes similar to those of *Chlamydomonas*. A cell functions as a

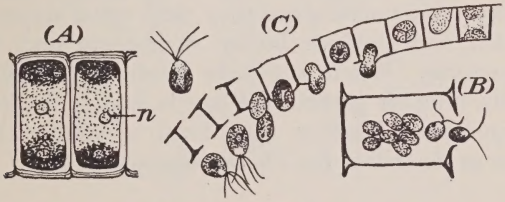

FIG. 196.—*Ulothrix*.

A, *U. zonata* (× 500) with pyrenoids and lamellated wall. *n*, nucleus. *B*, gametangium. *C*, *U. subtilis*, producing zoogonidia.

gametangium and its contents divide into sixteen or even thirty-two parts (Fig. 196, *B*). Each of these develops into a pear-shaped gamete with two cilia at its more pointed end, possesses a chloroplast and a pyrenoid and may have an eye-spot and two contractile vacuoles. After the rupture of the gametangial wall and the consequent liberation of the gametes, two gametes (probably from different plants) conjugate, a thick cell-wall is formed round the fused product, and a zygospore results. After a period of rest the zygospore germinates into a one-celled plant containing eight to sixteen zoospores. After these are liberated, they swim about for

some time by means of four cilia, but eventually come to rest and divide in one direction to form new filaments. When sexual reproduction occurs there is thus a kind of alternation of generations. The *Ulothrix* filaments are gametophytes, the gametes which they form fuse and, from the egg developed, a kind of primitive sporophyte with eight to sixteen spores is produced.

Asexual Reproduction. Under some conditions, some or any of the cells of the filament may divide and form similar bodies to the zoospores. As these are produced on the gametophyte and give rise directly to the gametophyte again (Fig. 201, *C*), they are often called **zoogonidia** (Fig. 196, *C*), and the reproduction is said to be asexual. The zoogonidia are similar to gametes but are larger, four-ciliate and are produced in less numbers in their mother-cells. Occasionally asexual reproductive bodies have no cilia and then they are simply termed gonidia. The sexual character of the gametes is not very pronounced since they may settle down without conjugation and produce bodies resembling and behaving like zygospores. When a gamete becomes an egg without union with another gamete the egg is said to be formed by parthenogenesis. *Ulothrix* may form a similar Palmella-condition as described for *Chlamydomonas*.

Spirogyra

Many species of *Spirogyra* are found in fresh water. One common species (*S. tenuissima*, Fig. 197, *B*) is often less than 14μ thick, whilst another species (*S. crassa*) is over 150μ thick. The thallus is an unbranched filament which is completely **septate** and has a slimy feel because there is a gelatinous investment outside the usual cellulose wall. Each cell has its protoplasm lining the cell wall, the central portion being occupied by a vacuole. The nucleus, which usually has one large nucleolus, may be closely attached to the protoplasmic lining but is usually more central in position and is attached to the lining by means of cytoplasmic threads. *Spirogyra* gets its name from the spiral way in which the chloroplast or chloroplasts are arranged.

In some species (e.g. *S. tenuissima*) there is only one chloroplast with three to six turns of the spiral (Fig. 197, *B*) whilst other species have two or more chloroplasts. *S. majuscula* often has five or more (Fig. 197, *A*), and each of them has only one or two windings. In this species the centrally-placed nucleus is usually very distinctly shown. The spiral chloroplasts contain denser portions which often become blue with iodine. These are pyrenoids and the blue color-

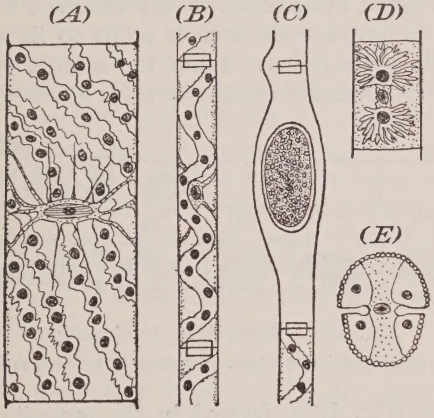

FIG. 197.—Optical views of Conjugatæ (× 250).

Nucleus shaded, nucleolus dark, pyrenoids darkened, cytoplasm dotted, chloroplasts outlined. *A*, single cell of *Spirogyra majuscula* with several chloroplasts. *B*, *S. tenuissima* with one chloroplast and with replicate ends to the cells. *C*, *S. inflata* showing lateral conjugation. Zygospore with oil globules. *D*, *Zygnema pectinatum* with stellate chloroplasts. *E*, Desmid (*Cosmarium*).

ation is due to the surrounding starch grains produced by their activity. There seems to be a division of labour in photosynthesis; the general body of the spiral chloroplast absorbs the light, and the energy thus obtained is used by the denser pyrenoids for the manufacture of starch.

Vegetative Reproduction. The vegetative division by which the number of cells in a filament increases usually occurs early in the morning. During the preceding day the cells have been storing up food, this is used for making fresh cells

in the first part of the day's work and then the cells concern themselves in preparing material for the next day's division. The filament therefore has an indefinite length but fragmentation into short chains of cells occurs, and each of these chains form new filaments by cell-division. In some species which are said to be **replicate,** an annular infolding of the transverse walls occurs and fragmentation is facilitated by the eversion of these infoldings (Fig. 197, *B* and *C*).

Sexual Reproduction. This occurs by means of gametes which are similar in appearance but different in behaviour. Two filaments arrange themselves so as to lie more or less parallel with one another. From the middle of one cell a protuberance is formed and extends till it meets with a similar

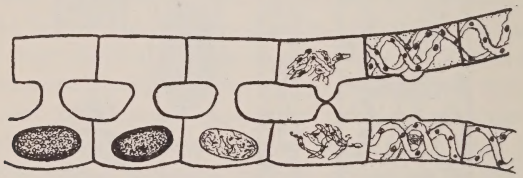

Fig. 198.—Scalariform Conjugation.

Spirogyra with two chloroplasts (× 250). Graphical conventions as in previous figure.

protuberance (Fig. 198), formed in the opposite cell of the parallel filament. The wall between the two protuberances is absorbed and a conjugation-canal is formed. In each of the two cells which are thus put into communication, the protoplasmic contents contract away from the cell wall, and function as a gamete. One of the gametes passes through the conjugation-canal and fuses with the gamete of the opposite cell. The resulting zygospore is usually more or less elliptical, at first has a green colour but later becomes brown and most of the starchy reserves are usually converted into oil. After a period of rest the zygospore germinates (Fig. 201, *A*), a reduction division occurs, and a new filament is formed directly.

The germination of the zygospore occurs in the same way as in the spore of a fern or a moss, the inner coat protrud-

ing as a short outgrowth through the outer covering. In the outgrowth a transverse wall is formed, the lower cell becomes a colourless attaching organ and the upper cell continues dividing to form the filament (Fig. 201, *A*).

Conjugation. The method of sexual reproduction is known as conjugation and, though there is little differentiation of structure between the gametes, the difference in behaviour justifies us in considering the active gamete as male and the passive as female. Any cell may function as a gametangium and usually all the cells in one filament function as male gametangia whilst those in the other function as female. The resemblance to a ladder shown by the two parallel filaments connected together by conjugating cells has suggested the name of **scalariform** conjugation. Another kind of conjugation, which is known as **lateral** conjugation, sometimes occurs. In this case two adjoining cells of the same filament are connected by a conjugation canal at their contiguous ends (Fig. 197, *C*). Occasionally the contents of a cell may become rounded off to form an egg-like body (**azygospore**) and this may be considered to be a kind of parthenogenesis.

Lack of Differentiation. One must notice that each cell of a filament is independent of other cells in regard to feeding and breathing and that any cell is capable of functioning as a gametangium. There is no alternation of generations, the gametes join to form the zygospore and this develops directly into a new gametophyte, so that the only indication of a sporophyte is the reduction division which occurs in the zygospore.

Conjugatæ. The order of algæ containing *Spirogyra* and other genera which have a similar method of sexual reproduction is known as Conjugatæ. In *Zygnema* the chloroplasts have a stellate appearance (Fig. 197, *D*), and in a few species the zygospore is formed in the conjugation-canal. As both gametes have approached each other there is no differentiation into male and female gametes in these species.

Desmids. The unicellular desmids (Fig. 197, *E*), so

remarkable for their beauty and diversity of form, have a similar method of conjugation and are therefore placed in the same order.

Vaucheria

The thallus of this alga, like *Ulothrix* and *Spirogyra*, is a filament but it shows a different vegetative structure and the reproductive bodies formed on it are much more highly developed (Fig. 199). Species of it are frequent during early spring or autumn in ponds, on soil of flower-pots and in cut cornfields during wet seasons. The terrestrial species cover the soil with a thickish tangle of green threads and, as mosses are often associated with them, may be mistaken for protonemal growths. It is not, like *Spirogyra*, confined to fresh water, as some species prefer brackish water and some are distinctly marine. The thallus is sparsely-branched, has a thickness varying from 50–200 μ, is sometimes as much as 30 cm. long, and never has septa developed except as a result of injury or during the growth of the reproductive organs. It is attached to its substratum by a kind of rhizoid or holdfast which is colourless and branched. The cellulose wall is rough to the touch, and has a protoplasmic lining within which is a central vacuole. Numerous small nuclei and many minute oil globules are present in the protoplasmic lining. Since the bodies containing chlorophyll are numerous and small, pyrenoids are not developed. The presence of oil, instead of starch, as a food-reserve is more characteristic of fungi than of algæ. A structure, like that of *Vaucheria*, in which the plant starts as a single cell and during its growth never produces any septa is said to be **cœnocytic.**

Gametangia. Reproduction is effected either sexually or asexually. The gametangia are **antheridia** and **oogonia** (Fig. 199), and are usually on the same plant, but some dicœcious species exist. In both antheridia and oogonia a cylindrical outgrowth of the thallus, containing many nuclei, oil globules and chloroplasts, is the first indication that a gametangium is developing, and then a septum separating the gametangium from the vegetative portion of the plant

is formed. In the oogonium all the nuclei, except one, go back into the main filament before the septum is formed, and the remaining nucleus forms the nucleus of the single oosphere. The oogonium swells and assumes an ovate form, with its narrower and free end forming a beak, which ruptures

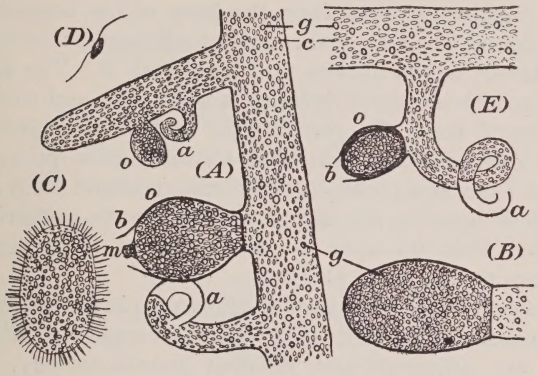

Fig. 199.—*Vaucheria.*

A, *Vaucheria sessilis*, main filament with oogonium and empty antheridium. Branch with young oogonium and antheridium × 100. *B*, zoogonidangium × 150. *C*, zoogonidium × 150. *D*, spermatozoid × 500. *E*, *V. terrestris* × 150. The branch bears an oogonium and an empty antheridium. *m*, mucilage; *o*, oogonium; *a*, antheridium; *b*, beak; *c*, chloroplasts; *g*, oil-globules.

and allows a small quantity of mucilaginous protoplasm to escape. The remaining protoplasm rounds itself off and forms the oosphere. The chloroplasts travel away from the beak towards the base of the oosphere so as to leave a colourless apical portion termed the receptive spot.

Formation of Spermatozoids. The nuclei of the antheridium do not travel into the main filament, though many of the chloroplasts do, but collect in the central portion of the antheridium, which is cut off by a septum from its stalk. The antheridium assumes a curved shape and its nuclei become the nuclei of the numerous spermatozoids. Each spermatozoid (Fig. 199, *D*) has two cilia which are arranged in an unusual way. Instead of being placed at one end, as in most algæ, there is one at each end. As in the oogonia, all

the protoplasm is not used up to form the gametes, some is expelled with the spermatozoids and some is left behind. This seems to indicate that a certain amount of selection goes on, and that any protoplasm which contains waste substances is rejected for gamete-formation.

Fertilization. The spermatozoids are apparently attracted to the mucilage exuded from the beak of the oogonium and cluster round it. One of them eventually enters the receptive spot, travels to the nucleus and fuses with it. The fertilized egg (zygote or oospore) develops a thick wall and can endure a prolonged rest. On germination it develops directly into a new Vaucheria filament. Self-fertilization is probably the rule but there is a possibility of a spermatozoid from another plant joining with the egg, especially as the antheridium is so coiled that its apex is often turned away from the oogonium on the same plant.

The orientation of the gametangia varies in different species. In *V. sessilis* (Fig. 199, *A*) they are on separate outgrowths which are adjacent and develop simultaneously. In *V. geminata* a branch gives rise to a central antheridium with two laterally-placed oogonia, and slightly different methods of arrangement occur in other species (Fig. 199, *E*).

Asexual Reproduction by Zoogonidia. After *Vaucheria* has been kept in darkness for some time and then exposed to light, zoogonidia are formed. The end of a filament becomes club-shaped and full of protoplasm richly supplied with nuclei, chloroplasts and oil-globules. A septum cuts this portion off from the rest of the filament (Fig. 199, *B*), and the protoplasmic mass escapes through a small apical opening, sometimes becoming so constricted as to divide into two portions. As its surface is beset with numerous cilia it is termed a zoogonidium (Fig. 199, *C*). It is able to germinate directly and usually produces a colourless outgrowth (**hapteron**) by which it attaches itself to the substratum.

Other Methods of Reproduction. A kind of fragmentation appears to be common in some species of *Vaucheria*. The contents of a filament escape (often as a result of injury) and more or less rounded amœboid masses, which may event-

ually develop into new filaments, are formed. Other forms of asexual and vegetative methods of reproduction occur during unfavourable conditions such as drought. The end of a filament swells up, and is then cut off as a gonidium. In another method the filament breaks up into a number of parts, each of which covers itself with a thick wall and forms a kind of **cyst.** Both the gonidium and cyst are resting bodies and, like the zoogonidium, have a cœnocytic structure.

Œdogonium

Œdogonium (Fig. 200) is another filamentous alga which inhabits fresh water. Its filaments are unbranched and in the young state are attached to stones or other objects at

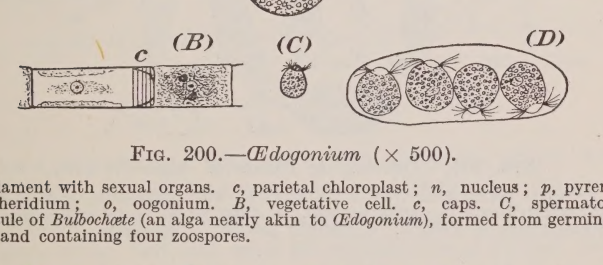

Fig. 200.—*Œdogonium* (× 500).

A, filament with sexual organs. *c*, parietal chloroplast; *n*, nucleus; *p*, pyrenoid; *a*, antheridium; *o*, oogonium. *B*, vegetative cell. *c*, caps. *C*, spermatozoid. *D*, capsule of *Bulbochæte* (an alga nearly akin to *Œdogonium*), formed from germinating zygote and containing four zoospores.

the bottom of the ditch or pool by means of colourless haptera, though they become free in older plants. The cells are longer than broad, have a protoplasmic lining enclosing a central vacuole and are uninucleate. One chloroplast is present in each cell and one or more pyrenoids are present.

Cap-Cells. Division is usually restricted to occasional cells, and as after each division a cap of cellulose is formed at one end of the mother-cell, these cells can be recognized by the transverse striations (caps) shown at one end (Fig. 200, *B*).

Zoogonidia. Asexual reproduction is effected by zoogonidia which differ from those of *Ulothrix* in having a circlet

of cilia at the colourless and more pointed anterior end. Any cell may function as a gonidial case (**gonidangium**); its protoplasm rounds itself off, and the green body escapes by a transverse split at the upper end of the gonidangium. Its method of germination is similar to that described for *Ulothrix* (Fig. 201, *B*).

Sexual Reproduction. This is effected by spermatozoids and oospheres (Fig. 200). A single cell becomes swollen to form a globular oogonium. Its contents are rounded off to form an oosphere and, at the clear receptive spot, mucilage is extruded by an opening due to a transverse split or to a pore. A spermatozoid is attracted to the mucilage, enters the oogonium and fuses with the oosphere. In monœcious species the antheridia are formed from short cells near to

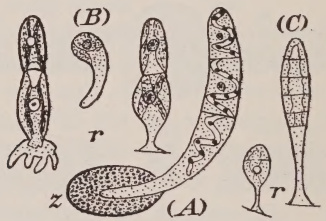

Fig. 201.—Developing Plants of Algæ (× 250).

A, *Spirogyra* germinating from a zygospore (*z*) with ornamented coat (position of rhizoid indicated as if in optical section). *B*, three young plants of *Œdogonium*. *C*, two young plants of *Ulothrix*. *r*, root-like portion; *z*, zygospore.

the oogonium, and from each antheridium one or two spermatozoids are formed. These are similar to the zoogonidia, but much smaller and yellower. Many species of *Œdogonium* are dicœcious, the male filament being as wide (or nearly so) as the female, but in some species (**nannandrous** or **gynandrosporous**) the male plant is very much smaller than the female. In these nannandrous species, peculiar zoogonidia (**androgonidia**) are found on the female plant in tabular cells similar to the antheridia. Each androgonidium is similar in structure to a zoogonidium or spermatozoid but intermediate in size. It moves to the female plant and

attaches itself on, or near to, an oogonium. On germination it produces a dwarf male plant, which usually consists of a "root-cell" and two or three tabular cells above it. The upper cells are antheridia and each produces a single spermatozoid.

Growth of Egg. After fertilization the zygote invests itself with a cell-wall and becomes brown. The oogonium containing the zygote separates from its filament, falls to the bottom of the water, and a resting period ensues. The contents of the zygote eventually issue forth in a thin gelatinous envelope, and divide into four zoospores (Fig. 200, *D*). The layer of jelly dissolves and the zoospores, which are similar in size, structure and behaviour to zoogonidia are set free.

Alternation of Generations. The plant is a potential gametophyte, though it often reproduces itself by vegetative

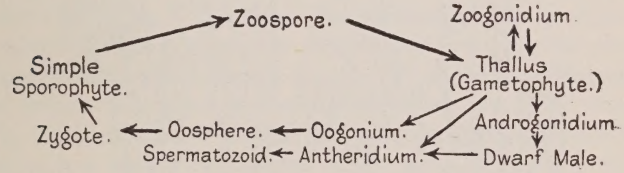

Fig. 202.—Life Cycle of *Œdogonium*.

or asexual means. The reduction division which results in the formation of four zoospores recalls the development of true spores, and therefore the gelatinous envelope and its contents (Fig. 200, *D*) may be regarded as a simple kind of sporophyte. The life-history of *Œdogonium* is represented in Fig. 202.

Fucus

All the algæ hitherto considered are unicellular, colonial or filamentous forms belonging to the class of green algæ (Chlorophyceæ) in which the colour is usually entirely due to chlorophyll. The highest vegetative development is shown in some brown algæ (Phæophyceæ) in which the chromoplasts have a brown colour, owing to the presence of another pigment in addition to those of chlorophyll. Some of the Phæophyceæ

such as *Ectocarpus* are filamentous but the familiar sea-wracks (*Fucus* and *Laminaria*) show much greater differentiation.

Habitat and Structure. One of the commonest sea-weeds is *Fucus vesiculosus* (Fig. 203), the twin bladder-wrack, so well known because of the paired air-bladders present on the thallus. It clothes the rocks between tide-marks, and has portions simulating roots, stem and leaves, though these

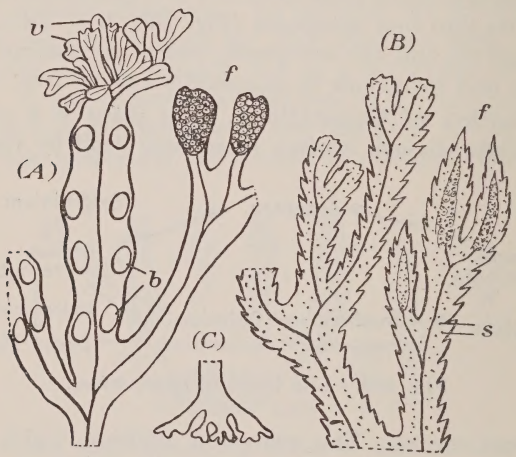

Fig. 203.—Brown Algæ.

A, Fucus vesiculosus. Portion of thallus with a group of somewhat crowded adventitious shoots (*v*) at the apex of one lobe and two fertile branches (*f*) with conceptacles terminating two other lobes. *b*, air-bladder. *B, F. serratus* with three groups (*f*) of fertile conceptacles and many scattered ones (*s*), most of which are sterile. *C*, attaching disc of *Laminaria* (that of *Fucus* is similar, but smaller and less branched). All figures reduced.

portions do not correspond to the similarly named organs in higher plants, and are merely modifications of the thallus. A certain amount of differentiation of the cells (Fig. 204, *A*) into epidermal, cortical and medullary regions occurs but this differentiation is far from complete, division may occur in any region, and a layer of cells in one region may form tissue similar to that of another region, e.g., the inner cells of the cortical region may add to the bulk of the medulla.

The "epidermal" cells are arranged like bricks end up, are meristematic, contain chlorophyll and form the chief assimilatory region. The cortical cells are parenchymatous, the chromoplasts are fewer, and form the main storage portion of the carbohydrate reserve. Starch is not formed, the reserve substance being another polysaccharid (laminarin) which does not become blue with iodine. In the medullary region the cells are longer and appear more like a tangled web of filaments (**hyphæ**). The cross-walls are often perforated in a sieve-plate manner, and this character, together with the elongation of the cells, leads us to consider that the main function of the central region is a conducting one. In *Laminaria*, the large strap-like sea-wrack, which is found on the rocks near low-tide level, distinct sieve-tubes, comparable to those of flowering plants, are developed.

Air-bladders. The leaf-like portion of the thallus has a midrib which is merely a thicker portion with the central tissue relatively greater and denser. On the sides of the midrib are hollow inflations of the thallus which are filled with air (Fig. 203). These air-bladders give buoyancy to the plant and, during low water, the renewal of the air in them may give a supply of oxygen for the plant when it is immersed later on. Air bladders are not formed in all species of *Fucus*, and are not restricted to this genus. In *F. serratus* (Fig. 203) they are absent, whilst in the well-known knotted wrack or sea-whistle (*Ascophyllum nodosum*) they are much larger than in any species of *Fucus*. They are also present in the gulf-weed (*Sargassum bacciferum*) and a few other brown sea-weeds. The intercellular spaces of the thallus do not contain air but mucilage, and this prevents the plant from being dried up during its exposure when the tide is out.

The stalk is formed from the midrib, the thinner marginal portions dying away whilst the cells in the midrib continue their meristematic activity. The disc or holdfast is a branched or disc-like body of similar structure and is formed from the divisions of the lower cell of the developing egg. It fixes the plant so firmly to the rock, that the latter is often dislodged when an attempt is made to pull the plant away. The pliant

nature of the stalk and its leaf-like flattened branches also tend to greater security of tenure.

Dichotomy. In *Fucus* and its allies the thallus increases in length by means of cells cut off from the base of a large apical cell. When a new lobe of the thallus is about to form, the apical cell divides longitudinally into two, and as each of these forms the apical cell of a new lobe, the branching is truly dichotomous.

Vegetative Reproduction. Small miniatures of a *Fucus* plant sometimes arise as adventitious shoots (Fig. 203). They are usually towards the base of the thallus and on separation may form new plants. This vegetative method is not frequent and the plant usually reproduces itself by sexual means.

Sexual Reproduction. The gametangia are formed in pits (**conceptacles**) of the thallus. These conceptacles

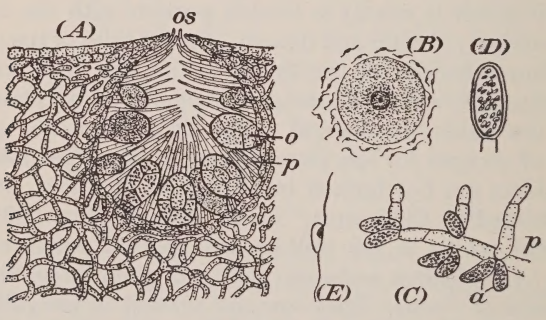

FIG. 204.—*F. vesiculosus* (× 40).

A, section of thallus through a conceptacle, in this case containing oogonia. *B*, oosphere (× 125), with spermatozoids clustered round it. *C*, antheridia from conceptacle of another plant (× 125). *D*, antheridium (× 250). *E*, spermatozoid (× 500). *a*, antheridia; *o*, oogonium; *os*, ostiole; *p*, paraphysis.

(Fig. 204) are, in most species, aggregated at the swollen ends of fertile shoots, and usually contain only one kind of gametangium. They communicate with the exterior by minute openings (**ostioles**) and contain many multicellular hairs in addition to the sexual organs. The antheridia are ovoid bodies borne on the multicellular hairs and, when

mature, are filled with spermatozoids and invested with two walls. The spermatozoid is a minute body provided with an orange chromoplast and having a cilium at each end (Fig. 204, *E*). The oogonia are larger and darker bodies fixed by short stalks to the base of the conceptacle and are interspersed with multicellular hairs (paraphyses). Each one has two walls and in *Fucus* contains eight oospheres. In *Pelvetia canaliculata*, a small Fucus-like plant growing near high-water mark, only two oospheres are present, whilst in *Ascophyllum* four are formed.

Fertilization. The outer walls of the gametangia are ruptured, the inner walls remain as sacs enclosing the spermatozoids or the oospheres, and the paraphyses become mucilaginous. The sacs containing the spermatozoids or oospheres are expelled through the ostioles, then the rupture occurs and the spermatozoids or the oospheres are liberated. A number of spermatozoids cluster round a spherical oosphere (Fig. 204, *B*) and cause it to rotate. Eventually one of the spermatozoids enters the oosphere, the two nuclei fuse together and a zygote is formed. This germinates without any resting period and divides into two cells, the lower of which branches to form the holdfast whilst the upper develops into the rest of the thallus.

Ascophyllum and most species of *Fucus* are dicœcious; *Pelvetia* and *Fucus platycarpus* are moncœcious, and the same conceptacle contains both antheridia and oogonia. There is no alternation of generations; the somatic cells are **diploid** (with 2 *n* chromosomes) and the reduction division occurs during the formation of the gametes.

General

The plant-body varies from a single cell in *Protococcus* (Fig. 191) to the many-celled thallus of *Fucus* (Fig. 204), and manufactures its own carbonaceous food. It never differentiates into stem and leaf and a true vascular system is absent, though sieve-tubes are present in *Laminaria*. Many kinds of vegetative, asexual and sexual reproduction are shown and motile gonidia, spores and gametes are common.

In heterogamous members the female gametangium is of a simpler nature than the archegonium of a moss or fern, it never has a neck and is known as an oogonium.

Classification. Most of the algæ which have been described are green in colour and belong to the Chlorophyceæ or group of green algæ. The brown sea-weeds, many of which have a much simpler thallus than *Fucus* or *Laminaria*, possess a yellow pigment (**phycoxanthin**) in addition to the pigments of chlorophyll and belong to the group Phæophyceæ. The diatoms also have the same pigments, but as they are unicellular or colonial and differ in many other respects from the Phæophyceæ they are often placed in a separate group (Diatomeæ). In the red algæ, which are almost exclusively marine, a red pigment (**phycoerythrin**), in addition to chlorophyll, is present. Their sexual organs differ widely from those which have been described in the types selected, and approximate to those which will be described later for lichens. On account of these differences they are placed in a separate group which is known as Rhodophyceæ or Florideæ. The blue-green algæ (Cyanophyceæ or Myxophyceæ) contain the blue-green pigment **phycocyanin** in addition to chlorophyll. They are unicellular or filamentous plants (see *Nostoc* in Fig. 225) which are frequently united into colonies by their gelatinous investments. The cells do not contain a definite nucleus, and a structure corresponding to a chloroplast is seldom found. Reproduction is chiefly by the fission of the cells, though resting spores occur in some species, and a sexual method is unknown. Further references to this primitive group will be found on pages 336 and 344.

CHAPTER XXX

THALLOPHYTA—FUNGI

The group of fungi is separated from the algal group by a single physiological character. The absence of chlorophyll causes them to be dependent on organic material for their supply of carbonaceous material. Most fungi also depend largely on organic material for their supply of nitrogen. In a broad sense, the term fungus includes bacteria, but these differ from the other fungi in many ways and are often placed in a class by themselves.

Parasitic Fungi. Many of the fungi are parasites and rob the animals or plants, which they infest, of their nutritive materials and cause serious injury, or even death, to them. Examples of parasites which are harmful to their hosts are the blight (*Phytophthora*) which destroys the potato crop, the salmon disease (*Saprolegnia*) which chokes up the gills of the fish, the white rust (*Albugo*) which deforms the shepherd's purse and other Cruciferæ, the damping-off fungus (*Pythium*) of cress, the false mildew (*Plasmopora*) of the vine, the mildew (*Sphærotheca*) which ruins the hop crop, the ergot (*Claviceps*) of rye, the vegetable caterpillar (*Cordyceps*) which transforms its animal namesake into a mummified case, the leaf-curl or bladder-plum disease (*Taphrina*) of the peach, the ringworm fungus (*Favus*), the rust (*Puccinia*) and smut (*Ustilago*) of wheat and other plants, the stink brand (*Tilletia*) which causes the grain of wheat to smell like decaying fish, the silver-leaf disease (*Stereum purpureum*) of the plum, and the razor-strop fungus (*Polyporus betulinus*) of the birch. The saprophyte *Merulius* causes the dry-rot of timber and many other saprophytes cause the decay of the food-substances of man.

Useful Fungi. On the other hand, there are many fungi which are of great use to us. The whole processes of decay are associated with saprophytic scavengers which give to soil its useful supply of humus ; yeasts are used in brewing and baking ; mycorhizæ (p. 175) are associated in a symbiotic and useful relationship with the roots of woody plants, and many of the larger fungi, though their direct nutritive value is small, are used as food.

Importance of Reproductive Structures. The fungi are chiefly distinguished from one another by their reproductive methods. The structures concerned with reproduction are those which are most noticeable, and in fact often are the only parts of the fungus which can be seen without detailed investigation. Mushrooms and toadstools are structures for forming and dispersing the minute reproductive cells, the vegetative portion being merely a web of threads which penetrate between the decaying organic particles present in the substratum.

Mycelium. The vegetative portion of a fungus is of a fairly uniform character, and a general description of it will apply, except for details, to most fungi. A number of branched and usually colourless filaments (hyphæ) are loosely entangled together and form a web-like structure which is termed a mycelium. The hyphæ penetrate between the particles of organic material or into the cell of the host by the aid of ferments (enzymes), dissolving the bodies which obstruct their passage and converting them into material which is readily assimilated. The hyphæ are often unseptate and cœnocytic, but more commonly transverse walls are formed, though the septation is often incomplete, two or more nuclei being found between two septa. The cell-wall (especially in young hyphæ) may consist of cellulose, but usually it does not become blue with Schultz solution. This material is often called fungus cellulose, but it is a complex substance containing nitrogen and similar to the chitin which forms the leg-cases of insects. The protoplasm in a young cell is a granular or reticulate mass and in the older cells forms a lining enclosing a large central vacuole. The nuclei are

usually minute, but seem to be similar in structure to those of other organisms, and usually to divide by mitosis. Starch is never formed, though some substance turning blue with iodine occasionally occurs. Oil and glycogen, the latter becoming deep brown with iodine, are the carbonaceous reserves whilst some protein material may also be present. Plastids are never present; if any colour is shown the pigment is generally confined to the cell-wall.

Reproduction. The reproductive methods are usually asexual. Sexual bodies occur in some fungi but in most fungi they are reduced or absent. The gametes may be similar or differentiated into male and female. The oosphere is formed in an oogonium, but a true antheridium producing ciliated spermatozoids is only found in the Monobleplaris family, a small family belonging to the order Oomycetes (see p. 320). When true fertilization occurs a reduction division takes place at some later stage.

Polymorphism. Some fungi are remarkable for their polymorphism, two, three or more forms, which differ from each other in some vegetative character, but more usually in some reproductive structure, occur in one and the same species. Some of the fungi, dealt with in more detail later, exhibit polymorphism. The rusts often show polymorphism. The rust of wheat (*Puccinia graminis*) has two kinds of spore-producing bodies on its grass host, these being summer-spores (**uredospores**) and winter spores (**teleutospores**). A teleutospore, after a period of rest, produces a small filament bearing four smaller spores (**basidiospores**), each of which is capable of developing on the leaf of the barberry to form a cluster-cup forming a fourth kind of spore (**æcidiospore**). The æcidiospore, in its turn, is carried to the wheat and causes it to bear the previously mentioned forms. Some rusts are remarkable for their biological specialization. Two rusts, growing on different hosts, may not show the slightest structural difference, but the spore of one is incapable of infecting the other host. Such species are known as **biological species.**

Saprophytism and Parasitism. The distinction between saprophytes and parasites is not always quite definite. A

fungus which is normally a saprophyte, may apparently abandon its saprophytic habit and function as a parasite. An instance of this is given later in connection with a *Mucor* which grows on grapes.

Mucor

The mould which gives a white appearance to neglected boots and many other organic materials is a saprophyte called *Mucor mucedo*. Material for ready examination can

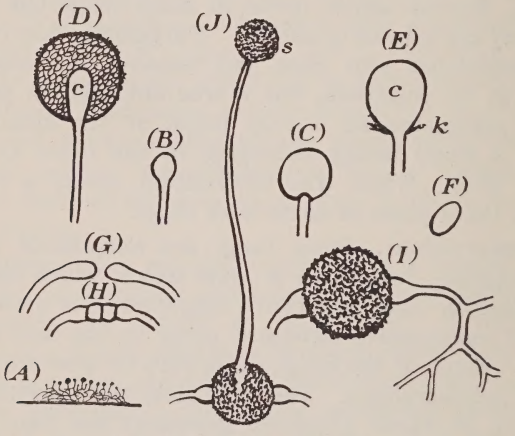

Fig. 205.—*Mucor mucedo.*

A, mycelium with gonidiophores and gonidangia (× 2). *B*, *C*, young gonidangia (× 100). *D*, mature gonidangium, optical L.S. (× 100) with gonidia and columella (*c*). *E*, burst gonidangium (× 100). *c*, columella; *k*, collar. *F*, gonidium (× 250). *G*, fertile hyphæ (× 100). *H*, fertile hyphæ with gametangia (× 100). *I*, zygospore (× 100). *J*, zygospore germinating to form promycelium with terminal sporangium (*s*) (× 50). *G–J*, after Brefeld.

easily be obtained by soaking a piece of bread (or horse dung) and then keeping it under a bell-jar. In a few days, if the temperature is a moderate one, little white specks appear, gradually spread and unite to form a mycelium (Fig. 205, *A*) of branched unseptate hyphæ, containing many small nuclei and oil globules. The cell-walls of the young portions give a blue coloration with iodine and strong sulphuric acid, but older parts do not show this reaction.

Production of Gonidia. Some hyphæ are negatively hydrotropic and stand out at right angles to the substratum, their tips swell and form a gonidangium, which is about 100 μ diameter when mature. A septum separates this from the rest of the hypha (**gonidiophore**) and its protoplasmic contents divide to form many ovoid gonidia. The pressure in the gonidiophore causes the septum to be pushed into the gonidangium. When rupture occurs the opposing pressure disappears, the top of the gonidiophore expands into a swollen portion (Fig. 205, *C*) which is called the **columella,** and the gonidia are liberated. The wall of the gonidangium is beset with crystals of calcium oxalate and some of these, with perhaps a remnant of the wall, form a collar round the base of the columella (Fig. 205, *k*). Each gonidium is capable of direct germination.

Conjugation. Sexual reproduction is of rare occurrence and the egg is formed by the conjugation of isogametes. Two hyphæ approach each other (Fig. 205, *G*), their apical portions are cut off by a septum to form gametangia, but there is no differentiation of the protoplasmic contents to form definite gametes. When the gametangia meet, the wall common to both is gradually absorbed and the contents fuse to form the zygospore (Fig. 205, *H* and *I*). The wall differentiates into two layers and the outer one becomes black. After the usual resting period, germination occurs and a simple or slightly branched dwarf plant (**promycelium**) is formed. The top of this swells out (Fig. 205, *J*) and produces a similar structure to the gonidangium. The bodies produced in this sporangium may be regarded as true spores and the promycelium as a simple sporophyte, though this view is not accepted by all botanists. The spore germinates directly into a normal mycelium.

Comparison may be made with *Spirogyra* which shows a similar method of conjugation, though no sporophyte is formed. Azygospores produced from a gamete without fusion with another were noted in *Spirogyra* and they are sometimes found in *Mucor*.

Some species of *Mucor* which occur on fruits are parasitic,

whilst others are able to act like parasites when the rind of the fruit is broken.

Vegetative Reproduction. When the mycelium is immersed in a nutritive solution the hyphæ may become septate and form chains of cells. When these cells are thick-walled they are resting cells (**chlamydospores**), but when their walls are thin they are capable of sprouting like yeast-cells (see p. 333) and of producing alcoholic fermentation.

Systematic Position. *Mucor* belongs to the class Phycomycetes in which some kind of sexual reproduction is normal and the vegetative body is usually a cœnocyte. The two principal orders of Phycomycetes are Zygomycetes with isogamous sexual reproduction and Oomycetes with heterogamous or oogamous reproduction. *Mucor* is an example of Zygomycetes whilst *Pythium*, the next fungus to be dealt with, is a member of the Oomycetes. *Rhizopus nigricans*, which is similar to *Mucor mucedo* but has a brown mycelium, *Pilolobolus crystallinus*, a pretty dung fungus in which the gonidangia are shot away from the columella, and *Empusa*, the house-fly parasite, are other common plants belonging to Zygomycetes.

Pythium

The seedlings of some plants are often attacked by a "damping off" fungus when conditions are suitable. The "damping-off" fungus (*Pythium debaryanum*) of cress may be readily obtained by growing cress-seedlings under a bell-jar, with an excessive quantity of water and an insufficient amount of air and light. The outer tissues near the base of the hypocotyl are attacked (Fig. 206, *A*), the mycelium penetrates into and between the cells and the seedling bends over. The mycelium is cœnocytic, similar to that of *Mucor*, and entrance into the tissues of the host may be effected by boring or through a stoma.

Asexual Reproduction. This is similar to that of *Mucor* but the gonidiophores may be short lateral branches, no

columella is formed, and the asexual spores are biciliate zoogonidia (Figs. 206–7). Under wet conditions the usual method of reproduction is by zoogonidia as these are able to swim about and rapidly infect neighbouring plants. Under drier and more unfavourable conditions the whole gonidangium may function as a gonidium (Fig. 207, *A*). In the

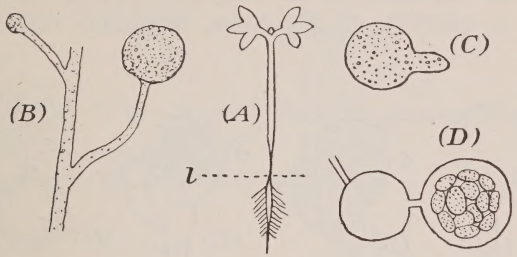

FIG. 206.—*Pythium*.

A, cress seedling attacked by *Pythium* just above level of soil (*l*). *B*, thallus portion with a young and an older gonidangium. *C*, gonidangium germinating. *D*, older gonidangium in which the papilla has enlarged and contains zoogonidia (after de Bary).

allied potato-blight (*Phytophthora*) the latter method is the commoner one.

Sexual Reproduction. This usually occurs when the conditions are likely to lead to the death of the fungus. Provision for the continuance of the race is made by the formation of thick-walled eggs which can rest for some time. During this process there is also a possibility of the two gametes coming from different plants, though, as we shall see, self-fertilization is the most probable. The gametangia are often formed at the tips of hyphæ but they may be intercalary, i.e. formed as lateral projections of the filament. Protoplasm streams towards these parts and its backward flow may be checked by the formation of septa. An oogonium (Fig. 207, *B*) is cut off by a septum from the swollen tip. As in *Vaucheria* there is a rounding-off of part of the protoplasm to form the uninucleate oosphere (Fig. 207, *C*), whilst the other nuclei pass into the unused protoplasm (**periplasm**). The antheridium (Fig. 207, *B*), or **pollinodium**, as it often is

termed, since it does not produce motile gametes, is formed on the same filament as the oogonium, or on a different filament. It is a club-shaped body and develops similarly to the oosphere, a septum cutting it off from the rest of the hypha and periplasm being formed. A little fertilizing tube is produced at the apex, and this penetrates through the wall of the oogonium to the oosphere. The fused product contains a quantity of oil-reserve, surrounds itself with a

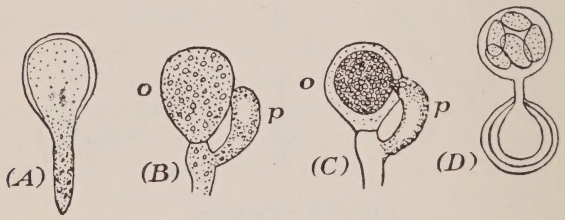

FIG. 207.—*Pythium*.

A, gonidangium functioning as a gonidium. *B*, oogonium (*o*), pollinodium (*p*) (× 800). *C*, oogonium forming oosphere and periplasm, and conjugation occurring. *D*, germinating zygote forming promycelium and zoosporangium (× 500). *B–D* after de Bary.

thick cell-wall and is an oospore, or zygote, capable of resting for a considerable period.

Germination of Egg. Germination takes place on contact with water, its method varies according to external conditions, and the first division of the zygote is a reduction division. Sometimes the zygote directly develops into a mycelium ; at other times a short hypha (promycelium) is produced and its end swells out to form a sporangium in which biciliate zoospores are formed (Fig. 207, *D*). In a third method the zygote itself functions as a sporangium, its contents dividing up into a number of zoospores. The zoospores are similar to the zoogonidia both in regard to structure and germination. The life-cycles of *Pythium* and *Vaucheria* are compared in Fig. 208. *Pythium* is truly parasitic and causes the death of the host. After this it is able to exist for some time in a saprophytic manner.

Allied Fungi. Other well-known members of Oomycetes

displaying more or less similar methods of reproduction are *Saprolegnia*, some species of which are saprophytic on decaying water plants and insects whilst others are parasitic on living fish, *Phytophthora infestans*, the potato-blight, *Plasmopora*, the false mildew of the vine, and *Albugo candida*, the white rust of the shepherd's purse. Some *Saprolegnias*

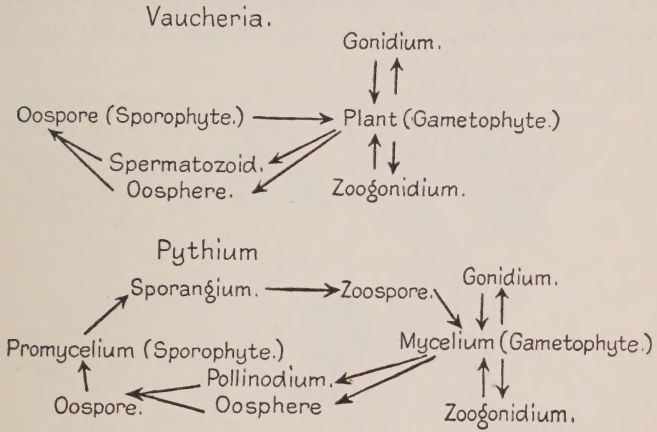

FIG. 208.—Comparison of Life Cycle of *Vaucheria* and *Pythium*.

are parthenogenetic, the unfertilized oosphere developing into the mycelium.

EUROTIUM

In the second group of fungi (Ascomycetes) there is one phase in the life-history in which non-motile spores (**ascospores**) are produced in a sporangium (**ascus**). These asci are usually formed in groups (**thecia**), and in some cases the tissues forming the thecium have been developed as the result of a sexual process. The ascus is usually flask-shaped and the number of ascospores contained in it is usually eight.

Production of Conidia. One of the simple forms of Ascomycetes, in which a sexual process can still be traced, is *Eurotium herbariorum*. When flowering plants are being prepared for the herbarium, they are pressed between sheets

of drying paper. Sometimes these sheets are not changed often enough and the damp plant is attacked by a mould. The mycelium is a much-branched, tangled mass of incompletely septate hyphæ, containing vacuolated protoplasm and oil globules. Some of the hyphæ become erect and the apices swell out to form spherical heads (Fig. 209). From each spherical head a number of rayed and divergent processes (**sterigmata**) arise. The apex of a sterigma swells out, fills

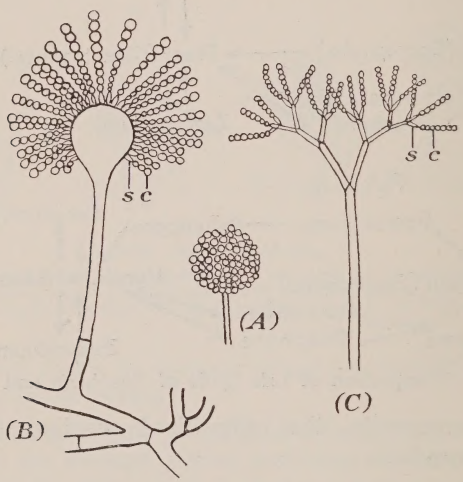

Fig. 209.—Asexual Reproduction in *Eurotium* and *Penicillium*.

Eurotium herbariorum. *A*, conidiophore (× 50), surface view; *B*, portion of mycelium bearing a conidiophore; sectional view (× 150). *C*, *Penicillium glaucum* (× 150). *s*, sterigma; *c*, conidium.

with protoplasm, and a spore-like body (**conidium**) is produced. This is separated by a narrow neck from the lower portion of the sterigma and another conidium is cut off. The same process is repeated and simultaneous development of neighbouring sterigmata goes on, so that in the end rayed chains of conidia (Fig. 209, *A* and *B*) are produced on the swollen end of the erect hypha (**conidiophore**). The end conidia are continually being abstricted and are minute, oval, greenish bodies, filled with protoplasm and oil globules. The

surface is somewhat spiny and there are the usual two coats, exosporium and endosporium. The conidium germinates in the usual way to form a mycelium. Owing to the glaucous hue of the conidia the plant was called *Aspergillus glaucus*.

Aspergillus and Eurotium. On the same badly-dried plants, besides *Aspergillus*, little yellow globes may be present, and these were thought to belong to an entirely different fungus, to which the name of *Eurotium herbariorum* was given. De Bary, to whom we owe much of our mycological knowledge, showed that *Aspergillus* and *Eurotium* were merely different stages in the life-history of the same fungus.

Production of Spores. The same mycelium which produces the chains of conidia develops the yellow globules

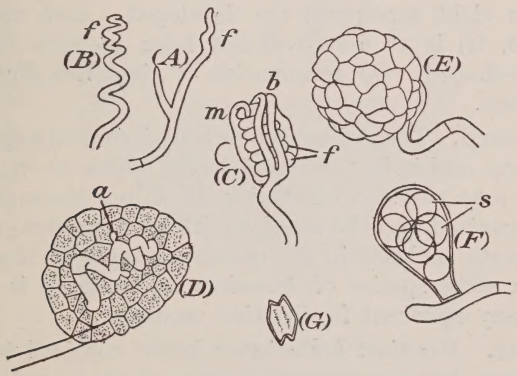

Fig. 210.—Development of Sporocarp of *Eurotium herbariorum*.

A and *B*, fertile hyphæ beginning to coil. *C*, archicarp with pollinodium (*m*) attached. Sterile hyphæ (*b*) are beginning to wrap round the archicarp (*f*). *D*, later stage (optical section) in which the sterile hyphæ have formed pseudoparenchyma around the developing sporocarp. *E*, ripe sporocarp (cleistothecium). *F*, ascus with ascospores. *G*, ripe ascospore (× about 75 except *F* and *G* which are × about 300). (After de Bary.) *a*, ascogenous hypha; *b*, sterile hyphæ; *f*, archicarp; *m*, pollinodium; *s*, ascospores.

by the following method (Fig. 210). A delicate hypha winds its end into four or five loose coils like a corkscrew and then the coils get nearer to each other so as to form a close spiral (**archicarp** or **ascogonium**). Several slender branches arise from beneath the archicarp. One of these grows faster

than the rest, arches over the top of the archicarp, and its contents probably travel to and fuse with the contents of the archicarp. The contents of the two conjugating hyphæ do not round themselves off into definite gametes, and actual fusion between them has not been observed. Sterile hyphæ wrap round (Fig. 210, *C*) and by septation form a **pseudo-parenchyma**, which encloses the whole body and packs itself between the coils. We may consider part of the contents of the archicarp as the female gamete, whilst the thread, which arches over it, is the pollinodium containing an undifferentiated male gamete. The fertilized archicarp becomes septate and forms little branches (**ascogenous hyphæ**). The ends of these are cut off by septa to form unicellular sporangia (asci). Each ascus (Fig. 210, *F*) is oval and by free-cell formation eight ascospores are developed. Each ascospore (Fig. 210, *G*) is at first oval but later becomes biconvex and boat-shaped. On germination it gives rise directly to a mycelium.

Sporocarp. The globose yellow body is termed a sporocarp or ascocarp, and in its formation sterile hyphæ as well as the gametes, take part. At maturity the filling tissue and asci are disorganized and the ascocarp (**cleistothecium**) consists of ascospores enclosed in the outermost layer of the former wall. In some species of *Eurotium* an ascocarp is formed without any apparent fertilization occurring.

Habitat. *Eurotium herbariorum* is not confined to badly dried plants, it occurs on many other substrata and is often an unbidden household guest on fruits and other decaying substances. It may be readily produced by putting a piece of damp (not soaked) bread under a bell-jar, and is often found on *Mucor* cultures when the bread is drying-up and the *Mucor* disappearing.

Penicillium. A common fungus similar to *Eurotium* is *Penicillium* (Fig. 209, *C*), the blue mould of cheese and other substances. The conidia are not produced in such a regular radiate manner. The top of the conidiophore branches in an irregular way and the mass of conidia, sterigmata, and the branches from which they are formed has a fan-shaped appear-

ance. In some species of *Penicillium* sporocarps or cleistothecia have been noted.

Lachnea

Groups of Ascomycetes. There are three main groups of Ascomycetes: (1) Plectomycetes, (2) Pyrenomycetes, (3) Discomycetes. Plectomycetes, to which *Eurotium* and *Penicillium* belong, include the relatively simple forms in which a closed ascocarp or cleistothecium is usually produced.

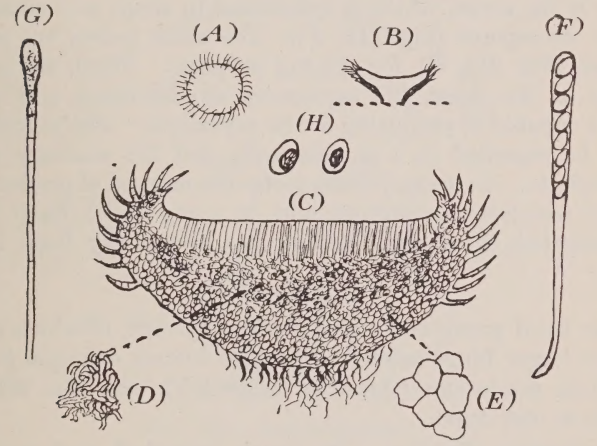

Fig. 211.—Discomycetes.

Lachnea, from cow-dung. *A*, surface view of scarlet ascophore or ascocarp (× 2). *B*, sectional view (× 2). *C*, section of ascophore (× 20). *D*, hypothecium (× 160). *E*, "cortical cells" (× 160). *F*, ascus (× 160). *G*, paraphysis with orange-coloured granules in clavate apex (× 160). *H*, two ascospores (× 210).

In Pyrenomycetes the ascocarp is a flask-shaped body (**perithecium**) which opens at the apex by a minute mouth (ostiole). The ergot of rye (*Claviceps*) and the vegetable caterpillar (*Cordyceps*) are members of this group. In the third group of Discomycetes the ascocarp (**apothecium**) is usually a larger body and at maturity is more or less disc- or cup-shaped with the asci-bearing portion well exposed.

Life History of Discomycetes. A species of *Lachnea* which

frequently occurs on cow-dung in autumn may be briefly described as an example of this third group. The septate hyphæ of the mycelium penetrate into the dung and obtain food from it. Sexual reproductive bodies approximating to what has been described for *Eurotium*, occur, and, though true fertilization may be abortive, an ascocarp (Fig. 211, *A* and *B*) is formed. This is an orange-red disc about 0·5 cm. in diameter and consists of pseudoparenchyma. The upper layer of cells forms the **hymenium** and contain two kinds of bodies which are vertically placed. One kind of body is the ascus, which is cylindrical in shape and contains eight ascospores (Fig. 211, *F*). The other bodies are paraphyses (Fig. 211, *G*), for spacing purposes. When the ascus opens at the apex, the ascospores are liberated and each one is capable of producing a new mycelium. The mycelium may be regarded as a gametophyte and the ascocarp as a sporophyte. In many Discomycetes the method of production of the ascocarp is unknown and, in many which have been investigated, the sexual method has apparently been lost.

Agaricus

The third group of fungi is Basidiomycetes, to which most of the larger fungi belong. The best known example is the common mushroom (*Agaricus campestris*), and this will be taken as our type.

Vegetative Portion. Its much branched and tangled mycelium obtains food from the humus of the soil. The hyphæ are colourless septate threads, each segment containing two nuclei. The protoplasm is vacuolated and oil globules are present.

Reproductive Portion. The edible portion above the ground is the reproductive body (Fig. 212). At maturity it consists of an umbrella-shaped cap (**pileus**) elevated on a stalk (**stipe**). Underneath the pileus are a number of radially-placed plates (**gills or lamellæ**) and about half-way down the stipe is a membranous ring (**annulus**). These structures develop in the following way. A little knob of densely interwoven hyphæ appears on the mycelium

(Fig. 212, 1), and as further growth occurs, develops into a young mushroom button. The upper part of the button expands to form the umbrella-like pileus whilst from the lower portion the stipe is gradually developed. The growth underneath the cap is not even, in some places new tissue is formed and in others growth is arrested. A space like a circular canal is formed (Fig. 212, 2–4) and on the roof of this chamber growth occurs in radial lines so as to form

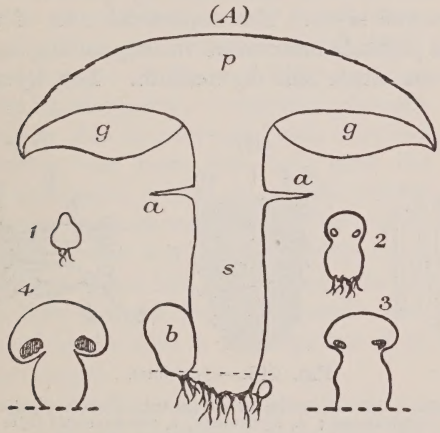

Fig. 212.—Basidiomycetes.

A, *Agaricus campestris* in section. *g*, gills; *a*, annulus; *p*, pileus; *s*, stipe; *b*, button. Dotted line represents surface of soil. 1, 2, 3, 4, development of a mushroom. Sections of four stages. In 1, no gill cavity is present.

the gills of the mature mushroom. The floor of the cavity is stretched owing to the outward expansion of the cap and the vertical expansion of the stalk and is ruptured. In the common mushrooms this rupture occurs quite near to the margin of the cap, and the remains of the gill-chamber floor are left as the membranous annulus (Fig. 212, *A*) on the stipe. In some " toad-stools " the rupture is not so clean and strips of the torn membrane hang from the margin of the pileus. In many other toadstools the tissue dries up so quickly during development, or after the rupture, that little

signs of the broken membrane can be seen, either on the stipe or on the margin of the cap.

Basidia and Basidiospores. The reproductive cells are produced on the gills and a certain amount of differentiation occurs in the tissues composing these. The middle of a gill consists of longitudinally arranged hyphæ (Fig. 213) which form a core (**trama**) of supporting and conducting cells. The outer cells of the trama curve outwards towards the surface of the gills and end in small, closely packed cells forming the sub-hymenial layer. The superficial cells of the gill are arranged in a palisade manner on the supporting sub-hymenial layer, and constitute the hymenium. The hymenial cells

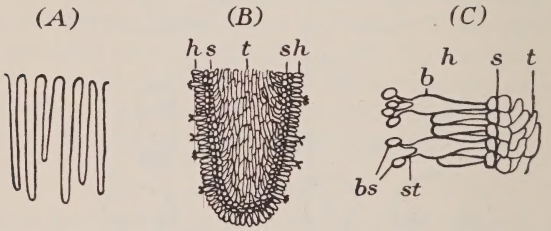

FIG. 213.—*Agaricus.*

A, section of gills (× 5). *B*, section of gill (× 60). *C*, portion of section (× 320). *b*, basidium; *bs*, basidiospores; *h*, hymenium; *s*, sub-hymenial layer; *st*, sterigma; *t*, trama.

are rich in protoplasm, and are club-shaped in form. Some of the slenderer cells (**paraphyses**) act merely as spacing or nutritive bodies whilst the stout ones (**basidia**) bear conidia (Fig. 213, *C*). Each basidium becomes uninucleate, and then four nuclei are produced by division. Four slender pegs (sterigmata) are produced at the free end of the basidium (Fig. 213, *C*), a nucleus passes into each of them, and their tips enlarge to form **basidiospores.** As each basidium produces four conidia or basidiospores and as there are thousands of basidia on each gill, the production of spores is enormous. By putting the cap of a mushroom, gill side downwards, on a sheet of paper, a dark gill-print is formed owing to the deposition of the innumerable spores. The

colour of the spores varies in different fungi ; in the mushroom the spores are brownish or purplish-brown, in the ink-cap (*Coprinus*) they are black. In many " toadstools " they are white, or pinkish, or yellowish and in a few cases even greenish ; if they are pale-coloured the gill-print should be made on a piece of black paper.

The basidiospores of the common mushroom are difficult to grow but, like those of other agarics, germinate directly into a new mycelium. There is no sexual method of reproduction and no alternation of generations. The young basidium contains two nuclei which fuse together and, during the division of the resulting nucleus into the four nuclei of the basidiospores, a reduction division occurs. This process may be due to a former habit, may indicate that the sexual process has been lost and that the basidiospore represents the spore, which in plants showing alternation of generations, germinates to form the gametophyte.

The tissue formed during the growth of the pileus and cap has an appearance like the parenchyma of a higher plant, but it has been formed from the growth and entanglement of aggregated hyphæ and is often spoken of as false tissue or pseudoparenchyma.

Edible and Poisonous Fungi. Many species of fungi besides the common mushroom are edible, in fact comparatively few of the gilled fungi are poisonous, but some contain deadly alkaloids and therefore great care must be exercised in the use of fungi as food.

Classification. The order of Basidiomycetes in which the basidia are formed on a superficial hymenium is called Hymenomycetes and include, not only the Agaricineæ or gilled species, but also other families in which the hymenium occurs on the sides of tubes, or of spines, or on the whole surface. The puff-balls, in which the hymenium occurs in many cavities inside the ball, is an example of the order Gasteromycetes. Rusts (Uredineæ) and smuts (Ustilagineæ) are members of two other orders.

CHAPTER XXXI

YEASTS—BACTERIA—LICHENS

Yeasts

Saccharomyces. The yeast fungus which is used in the manufacture of bread, beer and wine is called *Saccharomyces*. The brewer's-yeast (*S. cerevisiæ*) has cells which are almost spherical whilst those of the wine-yeast (*S. ellipsoideus*) are relatively longer. The yeasts are saprophytes and are able to excite alcoholic fermentation in a sugar solution. Pasteur's solution is a suitable medium in which yeast cells may be grown. It consists of 85 gms. of water, 15 gms. of grape sugar, 1 gm. of ammonium nitrate, 0·2 gm. of potassium dihydrogen phosphate (KH_2PO_4), 0·02 gm. of magnesium sulphate and 0·02 gm. of calcium phosphate ($Ca_3P_2O_8$).

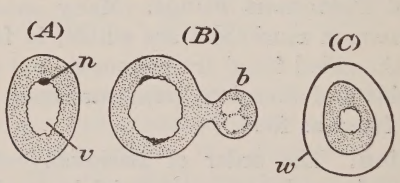

Fig. 214.—Yeast (*Saccharomyces cerevisiæ*, × 1000).

A, a single individual. *B*, budding cell. *C*, cell plasmolysed by 10 per cent. salt solution. The protoplasm has contracted away from the cell-wall, and the vacuole is reduced in size. *n*, nucleolus; *v*, vacuole; *b*, bud; *w*, cell-wall.

General Characters. The plant-body consists of a single cell (Fig. 214) or a group of cells which have not separated from one another. The cell-wall consists of fungus cellulose, is lined internally by the protoplasm containing proteid granules, glycogen vacuoles and oil globules, within

which is a large central vacuole. The nucleus is of a peculiar structure since its framework and nucleolus (Fig. 214, *A* and *B*) encircle the relatively large central vacuole.

Vegetative Reproduction. This goes on vigorously if the yeast is supplied with the right kind of nutritive solution. A little outgrowth appears, division occurs and the outgrowth enlarges (Fig. 214, *B*) till it becomes a replica of the parent-cell. The daughter-cells adhere to the parent-cells for some time and a chain or group of yeast cells may be formed (Fig. 215, *A*). This kind of vegetative reproduction is known as **budding, gemmation** or **pullulation.** The optimum temperature (other conditions being average ones) for this budding is from 25–35° C., the minimum is about 9° C., and the maximum about 60° C.

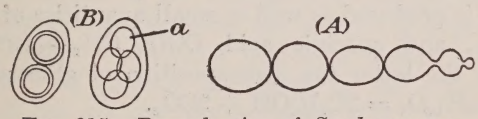

Fig. 215.—Reproduction of *Saccharomyces.*

A, chain of cells produced by budding, the daughter-cells still remaining attached. *B*, two asci. *a*, ascospore.

Asexual Reproduction. Under unfavourable conditions some of the cells become larger and function as sporangia. The nucleus of a sporangium divides into two to eight nuclei (usually four), each cell becomes invested by a firm, stout wall and forms a spore (Fig. 215, *B*). On the return of favourable conditions the exosporium breaks and budding recommences. Such unfavourable conditions as insufficiency of food when the yeast is left neglected in a jar or grown on damp plaster of Paris, or on a cut potato, usually cause this spore-formation to take place. Owing to the likeness of the method of spore-production to the free-cell formation which occurs in an ascus, the spores may be regarded as ascospores and the yeast plant may be considered as a degraded Ascomycetes.

Sexual Reproduction. In some species of *Saccharomyces* (*Zygosaccharomyces*) a kind of conjugation occurs between

two neighbouring yeast cells (Fig. 216). The conjugating cells are similar or nearly so. When the isogamy is perfect both cells put out conjugation-canals, but when one cell is larger, the contents of the smaller one pass into it. As a result of conjugation an ascus (Fig. 216, 5) is formed.

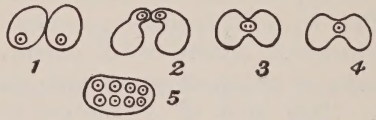

FIG. 216.—Conjugation and Formation of Ascospores in *Schizosaccharomyces octosporus*.

1, 2, 3, 4, stages in conjugation. 5, ascus with eight ascospores. (After Guilliermond.)

Alcoholic Fermentation. When yeast grows alcohol (C_2H_5OH) is produced as well as small quantities of glycerine $C_3H_5(OH)_3$, and succinic acid, $COOH.CH_2 — CH_2.COOH$. Neglecting the latter the decomposition of glucose may be given as $C_6H_{12}O_6 = 2C_2H_5OH + 2CO_2$.

EXPERIMENT 50. To show the production of alcohol in the higher plants. Place a dozen soaked peas and some pellets of moist blotting paper in a test-tube ; fill up with mercury and invert over a dish of mercury. After a few days test for alcohol : (*a*) smell, (*b*) odour on warming with sulphuric acid, (*c*) green coloration with potassium bichromate and strong sulphuric acid, (*d*) precipitation of iodoform with iodine and sodium hydroxide.

EXPERIMENT 51. To show the production of carbon dioxide and alcohol by yeast. Put a little yeast in a flask containing Pasteur's solution, fit a delivery-tube from it into a test-tube containing lime-water. Note the turbidity produced in the lime-water and test the liquid in the flask for alcohol.

EXPERIMENT 52. To show that sugar is necessary for the growth of yeast. Make up Pasteur's solution, omitting the sugar, and note whether any carbon dioxide is liberated or any alcohol formed.

EXPERIMENT 53. To show that yeast grows better in a warm solution than in a cold one. Half fill two similar flasks with tap-water containing glucose and a little yeast ; keep

one at a temperature of about 30° C. and the other at about 5° C. Compare the turbidities of the liquids in the two flasks after some time.

Experiment 54. To show that yeast can produce organic nitrogenous substance from inorganic nitrogenous material and a non-nitrogenous organic substance. Grow yeast in a solution of glucose in tap-water. Note the formation of new yeast cells and therefore of new organic nitrogenous substance.

Industrial Uses. Owing to the production of alcohol, yeast is used in brewing, and owing to the large amount of carbon dioxide produced, in the baking of bread. The flour is mixed with water and a little sugar solution containing yeast cells. Owing to the sticky nature of the proteid (**gluten**) of flour, a paste or dough is formed, and when the yeast "works," the starch of the flour is first changed into sugar and then this is acted upon by the yeast. A large amount of carbon dioxide is produced, and as it cannot escape the dough rises. On putting the dough in the oven the gas expands and the cavities become larger still.

Normal and Abnormal Methods of obtaining Energy. Most plants obtain their energy by the oxidation of carbon. If oxygen is withheld from soaked peas, they are still able to germinate to some extent and alcohol is produced (Expt. 50). The source of energy by which growth goes on cannot be the normal one, since the external supply of oxygen is cut off. The energy is obtained by the breaking down of complex compounds into simpler ones. If sugar is formed from carbon dioxide and water a great deal of energy must be expended, and when sugar is broken down into carbon dioxide and water, energy is liberated. The peas are not able to break down all the starch into these simple compounds, and some alcohol is produced. The equation representing this action may be given as $C_6H_{12}O_6 = 2C_2H_5OH + 2CO_2 +$ energy. In the germination of seeds without oxygen this method of obtaining energy is an abnormal one, whereas in the yeast plant it is the normal method. The tendency of yeast to excite fermentation is so strong that it occurs even when the food solution is well supplied with oxygen, though there is a greater amount

of alcohol and carbon dioxide produced when oxygen is absent. On the other hand, budding goes on more freely when oxygen is present, and then relatively little alcohol is produced. The ferment present in yeast cells and which induces the formation of alcohol is known as zymase.

Organisms which obtain their energy by the normal method are said to be **aerobic,** whilst those which are not dependent on an external supply of oxygen are said to be **anaerobic.**

Bacteria

The minute organisms, which are popularly known as germs or microbes, are sometimes included with the fungi since they do not contain chlorophyll, but they differ from the fungi in so many respects that they are better placed in a separate group of Thallophyta.

Fission. Their vegetative method of reproduction is by means of transverse division, the individual merely splitting into two parts and forming two individuals, so that they are termed Schizomycetes or Fission-fungi. As the blue-green algæ (Cyanophyceæ) also show this simple method of division, they are sometimes included with the bacteria to form a group known as Schizophyta. In some respects the bacteria approach to simple kinds of animals (Protozoa) and lie very near the boundary zone between animals and plants, in fact some "germs," which are usually referred to bacteria, are sometimes considered to be Protozoa similar to those which cause malaria, red water and sleeping sickness.

Structure. The plant-body (Figs. 217–9) is a colourless, minute, single cell which is rarely more than 5 μ long or more than 2 μ broad. The protoplasm may contain vacuoles, glycogen, proteid- and oil-bodies, but starch and chlorophyll are very rarely (if ever) present. Some bacteria contain material which becomes blue with iodine and a green pigment has been noted in a few species. Chromatin granules occur in some bacteria but they do not appear to form a definite nucleus. There seems to be a cell-wall of material slightly different to the protoplasm, but

if cilia come from it, as some bacteriologists maintain, it can only be considered as a slight modification of the more internal protoplasm. The difficulties in dealing with such minute

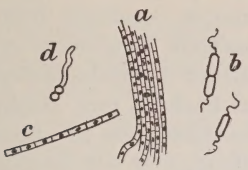

Fig. 217.—Bacteria. *Bacillus subtilis* (× 750). (After Sachs.)

a, zooglea condition; *b*, motile condition; *c*, with endospores; *d*, arthrospore of *Vibria cholerœ* (× 750). (After Hüppe.)

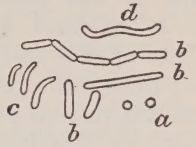

Fig. 218.—Different Forms of Bacteria (× about 1000). (After Buchner.)

a, *Micrococcus*; *b*, *Bacillus* and *Bacterium*; *c*, comma form; *d*, *Spirillum*.

bodies are so great that it is almost impossible to make definite statements on some points.

The shapes assumed by bacteria are variable (Fig. 218). *Micrococcus* and *Streptococcus* are spherical, *Bacterium* and *Bacillus* are rod-like, *Vibrio* is comma-like and *Spirillum* is wavy like a screw (Fig. 218, *d*). The disposition of the cilia in motile forms is exemplified by Fig. 219.

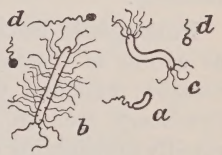

Fig. 219.—Ciliated Bacteria (× about 1000). (After Fischer.)

a, *Vibrio cholerœ*; *b*, *Bacterium vulgare*; *c*, *Spirillum undulum*; *d*, *Nitrosomonas*.

Habitat and Distribution. They occur in every part of the world, and in almost any situation where organic material is present, some being able to survive temperatures below freezing point whilst others (**thermopile bacteria**) are able to live in hot springs. The bacteria, whose activity cause the heating of beds of hay and manure, can live at a temperature of 60–70° C., but most bacteria (except when in the spore stage) are killed at a temperature of 50° C. Many species are anaerobic and obtain their energy in the same way as yeast does (p. 335).

Saprophytic Bacteria. Some species are saprophytic,

others are parasitic or live in symbiotic relationship with other plants. The decomposition of organic matter, so that the carbon is again brought into circulation as carbon dioxide, is largely accomplished by saprophytic bacteria. In addition to this action the ammonia resulting from such decay is oxidized by nitrite-bacteria (*Nitrosomonas*, Fig. 219, *d*) to nitrites and then the nitrate-bacteria (*Nitrobacter*) convert these into nitrates. Some bacteria (e.g. *Azotobacter*) increase the amount of nitrogenous substances on unmanured grassland by forming organic nitrogenous compounds from carbohydrate and the free nitrogen of the air. The retting of flax, the curing of tobacco, the souring of milk, the production of rancidity in butter, the conversion of alcohol into vinegar, the putrefaction of meat, the maturing of cheese and the conversion of sewage, etc., are accomplished by saprophytic bacteria, in some cases by themselves, in others with the aid of fungi. Most of these changes are brought about by some ferment, which is contained in, or produced by, the bacterial cell, e.g. an oxidase is present in nitrifying bacteria.

Pathogenic Bacteria. Parasitic bacteria are well known as causes of diseases. Such diseases as diphtheria, mumps, measles, typhoid, cholera, anthrax, influenza, tuberculosis, dysentery, etc., are caused by bacteria (pathogenic bacteria) rapidly multiplying in the body and producing toxic substances which poison the body cells. If these toxic substances cannot be dealt with by the white corpuscles of the blood or the body cells, and neutralized by an opposing substance (**antitoxin**), the patient dies. If the host is able to cope with the parasite and recovers, a certain amount of immunity from attack by the same parasite is obtained. This may be partly due to the using up of a particular pabulum necessary to the parasite and partly to the addition of some substance inimical to it. The body cells of the host are supposed to react to the toxic substance of the bacterium, and to produce an antitoxin. Any further attack by the same bacterium is unable to reach the body cells as the toxin is neutralized by the antitoxin present in the liquid plasma of the blood

or lymph. This antitoxic theory gives some explanation of the fact that when the serum of an immune animal is injected into another animal, the latter also becomes similarly immune.

Symbiotic Bacteria. Some bacteria live in symbiotic partnership with some other organism. *Bacterium radicicola*, which occurs in the root-nodules of leguminous plants, has already been mentioned on p. 75. The ginger-beer plant, or Californian bees, is a symbiotic partnership between a yeast and one or more bacteria. The bacterium uses the substances produced by the activity of the yeast and prevents their accumulation from interfering with that activity.

Hay-bacillus. One of the most readily available bacteria for examination is *Bacillus subtilis* (Fig. 217). This is a saprophyte which is found in an infusion of hay. It is a minute, rod-shaped body, about $5 \times 1\ \mu$, and is able to move by means of cilia. It reproduces actively by fission, and the individuals separate from each other and move about in the liquid. After some time, the individual cells produced by fission do not separate, but remain attached, so that a filament is formed. An immense number of these filaments aggregate together at the surface to form a scum and this state is termed the **zooglea** condition (Fig. 217, *a*). This is a resting condition since the cilia have been withdrawn, and after a time spores are formed. These are called **endospores** since they are formed inside the cells, all the protoplasm being used up, so that the filaments merely consist of cases, each with a thick-walled endospore in the centre. The endospore is able to withstand considerable environmental changes, and may even be boiled for over an hour without being killed. On germination the outer membrane is split and the contents form an ordinary bacillus cell. Endospores are formed by most bacteria (species of *Bacillus*) but sometimes the spore (**arthrospore**) is constricted off at one end (Fig. 217, *d*), as in the species belonging to the genus *Bacterium*, when this generic name is used in its strict and limited sense. There are differences in detail between the structure described for *B. subtilis* and that of other bacteria, but morphological

differentiation is slight. On the other hand, biological differences are considerable; for instance, some species which multiply rapidly in the body of one animal are incapable of affecting another one.

Filamentous Bacteria. In a few bacteria the filamentous condition is more permanent. The iron bacteria (e.g. *Chlamydothrix ochracea*), which form beds of limonite (hydrated ferric oxide) or bog-iron ore on lake bottoms, and the sulphur bacteria (e.g. *Beggiatoa alba*) which obtain their energy by the oxidation of sulphuretted hydrogen to sulphur, belong to this peculiar group.

Methods of Culture. Bacteria can be grown on culture materials, such as gelatine or agar-agar, and their various points of difference studied. As spores of many kinds of bacteria are present in the air a culture may consist of many kinds of bacteria and other organisms. Koch devised a method whereby pure cultures of a particular bacterium or fungus can be obtained and this has proved of great service to humanity. A little material containing the organisms is placed in a large amount of sterilized gelatine and then liquefied by warming. The material is then poured out on a plate so that the individual bacteria are isolated and each kind has its own centre of growth. As pure a patch as possible is picked out and the process repeated till a pure culture of the required bacterium is obtained.

Lichens

The symbiotic nature of a lichen has already been alluded to in Chapter XIX. An orange-yellow lichen, *Xanthoria parietina*, which is common and widely distributed on walls, stumps, trees and even on painted iron pillars, may be taken as a type.

Xanthoria. The thallus (Fig. 220) is more or less orbicular in outline, is closely adherent to the substratum and varies in size according to age. Some young thalli are less than 1 cm. in diameter whilst older plants may be many centimetres broad. Owing to the contiguous growth of several thalli,

the orbicular outline may be lost and an effuse patch 30 or more centimetres in length may be formed. The thallus is composed of many lobes, often overlapping each other

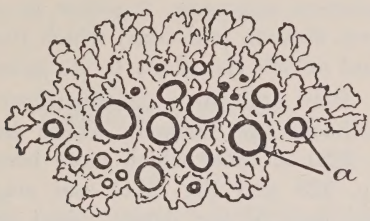

FIG. 220.—Foliaceous Lichen.

Thallus of *Xanthoria parietina* with numerous apothecia (*a*) (× 3).

and coloured with a yellow substance (**parietin**) which turns purple on the application of strong potash solution. A section of the thallus (Fig. 221, *A*) shows that it is mainly

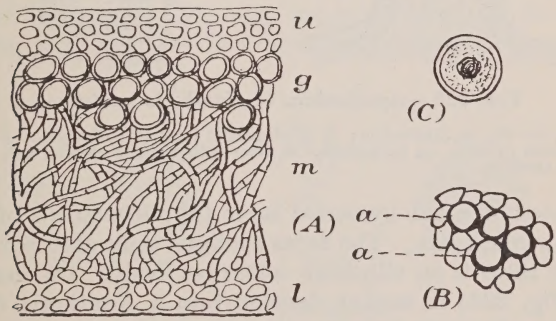

FIG. 221.—*Xanthoria parietina.*

A, T.S. of thallus (× 400); *g*, algal layer; *l*, lower cortex; *m*, medulla; *h*, hymenium; *s*, sub-hymenial layer (hypothecium); *u*, upper cortex; *B*, soredium, four algal cells (*a*) with fungal hyphæ round them (× 400). *C*, algal cell (× 800).

composed of interlacing, septate and branching fungal hyphæ. On the upper surface these hyphæ are so closely intertwined that they form a pseudoparenchymatous cortex (Fig. 221,*u*). Below this is the **gonidial layer** consisting of loosely-inter-

woven hyphæ with algal cells between them. The medulla (Fig. 221, *m*) is formed by loosely-interwoven hyphæ, and these become more compact towards the lower surface to form a cortex similar to that of the upper surface. At intervals medullary filaments aggregate together in a longitudinal manner and form strands (**rhizinæ**) which pass through the lower cortex and attach the plant to its substratum.

Apothecia. Here and there on the upper surface ascophores or apothecia are formed. These have a similar structure (Fig. 222) to those which have been described in *Lachnea* (see p. 328 and Fig. 211) and originate entirely from the fungal part of the lichen. Asci and paraphyses

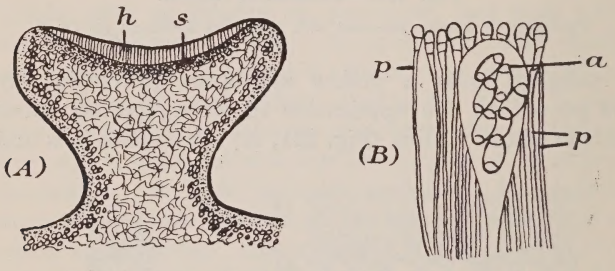

Fig. 222.—Apothecium of *Xanthoria parietina*.

A, L.S. (× 30). *h*, hymenium; *s*, sub-hymenial layer (hypothecium). *B*, portion of hymenium (× 330). *p*, paraphyses. *a*, ascus with eight ascospores, only seven of which are showing.

are seated on a sub-hymenial layer (**hypothecium**) of small pseudoparenchyma. The ascus contains eight ascospores and each of these is an elliptical colourless body. On germination (Fig. 223) it cannot develop into a Xanthoria thallus unless the filament produced meets with its appropriate kind of alga.

Soredia. When few apothecia are present on the thallus, vegetative reproductive bodies (Fig. 221, *B*) are often abundant. These are called soredia and consist of fungal hyphæ wrapping round and enclosing a few algal cells. As both constituents of the lichen are present in the soredium, it is able to develop directly into the Xanthoria plant.

Many other lichens besides *Xanthoria* are of a **foliaceous** character and exhibit a similar structure. A tree-like or **fruticose** habit is shown by *Ramalina*, *Usnea* (Fig. 122), etc., and modifications of the cortex or medulla in order to obtain the necessary rigidity are met with, but the essential

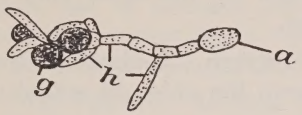

Fig. 223.—Germination of a Lichen Ascospore.

a, ascospore; *g*, algal cell; *h*, fungal hyphæ.

structure is similar to that of *Xanthoria*. A very large number of lichens show a much more primitive structure. In **crustaceous** lichens there is no lower cortex, the medullary hyphæ merely spreading out on the surface of the substratum or penetrating into it.

Algal Symbiont. The alga present in the gonidial layer is usually some member of Protococcaceæ, and is always the

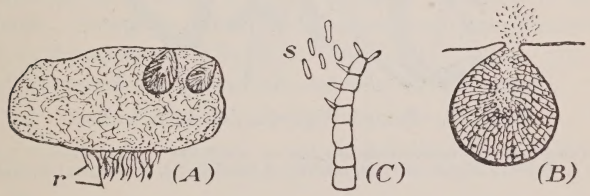

Fig. 224.—Spermogonia.

A, section of *Collema pulposum*, a gelatinous lichen in which fungal filaments and chains of algal cells (*Nostoc*) are embedded in mucilage (× 7). Two spermogonia are present towards the upper surface of the thallus. *B*, spermogonium discharging spermatia through the minute ostiole (× 60). *r*, rhizinæ. *C*, sterigmata and spermatia (*s*) (× about 400).

same for a particular species of lichen. The algal symbiont in *Graphis* and some other lichens is the reddish *Trentepohlia* and in most gelatinous lichens (e.g. *Collema*) it is the blue-green *Nostoc*. In some gelatinous lichens as *Collema* there

are no cortices, the fungal filaments and *Nostoc* threads being intermingled in a gelatinous medium (Figs. 224–5).

Perithecia. The reproductive cups are mostly apothecia but the large group of lichens to which *Verrucaria* belongs, bear perithecia opening by minute ostioles. The shape, size, colour and septation of the spore vary according to the constituent fungus.

Sexual Reproduction. Indications that the apothecia may be formed from the union of sexual cells, or that this

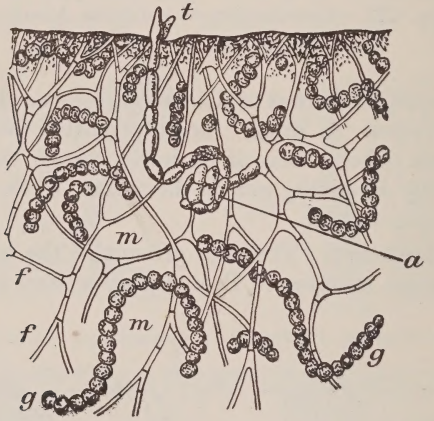

Fig. 225.—Sexual Reproduction in a Lichen.

T.S. of thallus of *Collema microphyllum* Ach. (× about 500). (After Stahl.) *f*, fungal hyphæ; *g*, chains of *Nostoc* cells; *m*, position of mucilage; *t*, trichogyne; *a*, archicarp.

process has been lost, are afforded by many lichens. In some cases a sexual process has been described. In *Collema* (Fig. 224) flask-shaped bodies (**spermogonia**) are sunk in the tissue of the thallus. At right angles to the bases and sides of the cavity filaments (**sterigmata**) arise and rod-like bodies (**spermatia**) are abstricted (Fig. 224, *B*). Stahl described a conjugating process as occurring between a spermatium and a filament (**trichogyne**) which projected from the surface of the thallus. He considered that the spermatium

was a male cell and that the trichogyne (Fig. 225, *t*) conducted it to a coiled female cell (ascogonium or archicarp) in the tissue of the thallus, then fertilization occurred and an apothecium was developed. A similar process has been described in other lichens by later observers ; ascogonia and even trichogynes have been shown to occur in a number of lichens, whilst spermogonia are of common occurrence. In most lichens these structures appear to be functionless relics of a former sexual method of reproduction.

Habitat and Distribution. Lichens are found in every part of the world and on almost any substratum. In the arctic and alpine regions they occur when other plants have ceased to exist. As their requirements are extremely small, they can often grow on such hard rocks as granite, where their nutriment must be derived from the atmosphere. A few lichens such as *Verrucaria maura* and *Lichina confinis* occur on the rocks in the tidal zone. On newly-exposed rocks such as the broken cliff side, or the shingle cast up on the beach, lichens are the first plants to appear, and in many other instances they may be considered as the pioneers of vegetation.

Industrial Uses. Dyes have been obtained from many lichens ; litmus is obtained from the maritime *Roccella*, and the reindeer-moss (*Cladonia rangiferina*) forms the staple food of reindeers at certain seasons of the year.

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